BIRDS OF THE LOWLAND PINE SAVANNA OF NORTHEASTERN NICARAGUA

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Although Central America has been investigated by biologists and worked by professional collectors for over a century, the region includes a large area of distinctive habitat that has remained almost unknown zoologically until recent years. This pine savanna includes only a single species of pine, *Pinus caribaea*; the region resembles the pinelands of British Honduras, but is entirely of low relief—generally less than 100 m above sea level. The Mosquitia is effectively isolated from the British Honduras pinelands and from the highland pine forests of Honduras and north-central Nicaragua by wide expanses of humid, lowland, tropical, broad-leafed forest. The approximate extent of the savanna is shown in figure 1; the southern extent of this habitat, between Laguna de Perlas and Bluefields, Nicaragua, marks the southern limit of naturally occurring pines in the Western Hemisphere.

The paucity of published biological information on the Mosquitia until the past few years is striking. The few visits made by ornithologists to the Nicaraguan area up to 1963 have been discussed by Howell (1965). Studies by Parsons (1955), Radley (1960), Johannessen (1963), Taylor (1963), and Munro (1966) provide valuable information on the geography and ecology of the region; the most recent zoological studies dealing with the pine savanna are those of Monroe (1968) in Honduras, Howell (1965), Campbell and Howell (1965), Monroe and Howell (1966), and Buchanan and Howell (1965).

From 1963 to 1967, my associates and I made five visits to the Nicaraguan savanna region, as follows: 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. The personnel included O. M. Buchanan, L. F. Kiff, M. B. Lloyd, F. G. Stiles, and J. E. Zoeger. These visits included periods in both the wet and dry seasons, periods when some spring and fall transients and winter residents were present, and periods when breeding birds that are not year-round residents were present. In another paper (Howell 1971), I have given a detailed account of ecological conditions in the pine savanna and the adjacent broad-leafed forest and have discussed species diversity, population density, intra- and interspecific competition, and niche utilization in the birds of these contrasting habitats. This paper deals primarily with the taxonomy, distribution, and reproductive biology of those species that use the distinctive features of the pine savanna in some ecologically important way—i.e., foraging, feeding, resting, nesting—with at least some regularity. I have therefore not listed every species recorded in or over the savanna, but have included some that may not use the savanna regularly or importantly but which are of distributional or taxonomic interest.

Those species using the savanna importantly may be categorized as follows:

Permanent residents—resident species whose presence depends on the presence of the savanna, which carry on most or all of their activities there, and which are absent from adjacent areas of broad-leafed forest.

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—differ from permanent residents only by their absence during the period from November to March, at least.

Winter residents—species that nest in temperate North America and are found 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, but which regularly range into the savanna and may even nest in the pines; however, all these species depend on the adjacent broad-leafed forest for many or most of their activities.

Passage migrants—spring or fall transients that pass through the savanna.

These categories may be abbreviated as PR, WrR, SR, WR, RV, and M, respectively, and these abbreviations are used where applicable in the species accounts. Equivocal cases and

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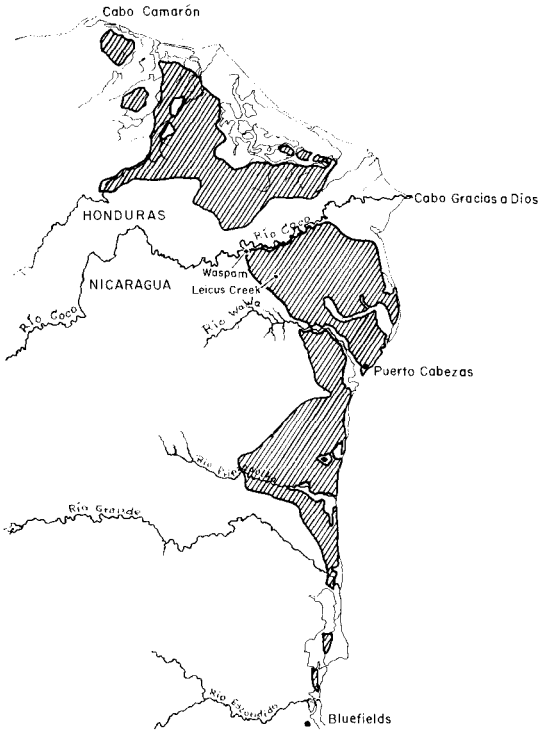

FIGURE 1. Extent of the lowland pine savanna in the Mosquitia of Honduras and Nicaragua.

species of uncertain status are discussed individually. Species recorded by sight only are indicated by an asterisk.

Localities and units—There are problems in the accurate designation of collecting sites and the spelling of place names in the savanna region (Howell 1965, 1966). Figure 1 includes the reference locations used in designating such sites. Our headquarters from 1963 to 1967 was a rosin-extracting plant at Leicus Creek, 56 miles northwest of Puerto Cabezas, and this locality is usually found only on recent, large-scale maps of the area. However, as the savanna habitat is relatively uniform throughout its extent, specific localities are not listed except for records of unusual distributional interest.

In the following accounts, all measurements are in millimeters and all weights are in grams unless otherwise designated. The English names and the sequence of species are based primarily on Eisenmann (1955) and Meyer de Schauensee (1966).

SPECIES ACCOUNTS

Podilymbus podiceps. *Pied-billed Grebe. We saw a single bird regularly during March and November 1966 in a small artificial pond at Leicus Creek. I know of no other record from Nicaragua although the occurrence is not unexpected.

Jabiru mycteria. *Jabiru Stork. We saw two of these birds together as they alternately flapped and soared over the savanna on 10 March 1966 about 30 miles NW of Puerto Cabezas. This species may be of rare but regular occurrence.

Bubuculus ibis. Cattle Egret. The first specimen record for Nicaragua is a male taken from a flock of six birds at Puerto Cabezas on 28 January 1962. The stomach contained ticks, spiders, and grasshoppers, and the testes were 10 mm long. In subsequent years, we saw Cattle Egrets at all seasons almost everywhere in the savanna where livestock was numerous, but no nests were found. The species is now country-wide in distribution.

Cathartes aura. *Turkey Vulture. WrR. This ubiquitous species is common at all seasons throughout the savanna.

Cathartes burrovianus. *Lesser Yellow-headed Vulture. We first recognized this species at Puerto Cabezas on 18 August 1965, and saw several there on 18 November 1966. I know of no other records for Nicaragua.

Coragyps atratus. *Black Vulture. WrR. These birds are common at all seasons throughout the savanna, especially near towns and villages.

Buteo albicaudatus hypospodius. White-tailed Hawk. PR. We recorded this species at all seasons and there is surely a resident population although no nests were found. The following specimens were obtained: ad. ♂, 8 February 1962; testes 10 × 3; ad. ♀, 13 February 1962; four follicles were enlarged to at least 5 mm; this bird was foraging at the edge of a grass fire, and the stomach contained remains of frogs, a snake, a lizard, and mammal hair. Colors of unfeathered parts of both these adults were identical and noted by Buchanan as: "iris dull zinc yellow; bill brownish black distally, blue-gray proximally; cere pea green; orbital skin light yellowish green; tarsi and toes bright zinc yellow." Young birds in generally blackish plumage were obtained as follows: ♀, 8 February 1962; ovary double, the right one smaller than left, follicles 1 mm in diameter; stomach contents, lizard remains; colors of unfeathered parts: iris buffy gray, other colors as in adults, but duller; ♀, 23 August 1965; follicles less than 1 mm; moderately fat; iris dark; plumage almost uniformly black ventrally, the feathers with some buffy edgings and largely concealed white bases; ♀, 28 November 1966; wt. 984; largest follicles 1.5 mm. White-tailed Hawks were not numerous enough to be seen daily but were not as scarce as Red-tails (see below). Grass fires attracted White-tails, as noted by Stevenson and Meitzen (1946) in Texas prairies where the prey species are similar. There are no previous published records of this species from Nicaragua although its occurrence there was expected.

Buteo jamaicensis kemsiesi. Red-tailed Hawk. PR. A series of five adults shows that a population of *kemsiesi* breeds in the savanna, extending the known range from the Nicaraguan highlands (Storer 1962). Specimens are: ♂, 30 January 1962, testes 12 × ?; ♂, 22 January 1963, testes 15 × 9; ♂, 23 January 1963; ♀, 16 February 1962, with five enlarged follicles measuring 21 (1), 12 (1), and 9 mm (3); ♀, 14 March 1966, wt. 1027, largest follicles 1.5 mm. The stomachs of all these were empty or contained unidentified matter. The data on gonad size indicate that breeding occurs early in the year, but no nests were found. We saw these birds at all seasons but the total sight records number only about 10.

Elanus leucurus. *White-tailed Kite. We saw one soaring over the pines on 31 January 1962 but saw none in the savanna region on subsequent visits. This species was first recorded in Nicaragua in 1961 (Bond 1964) and is now found regularly during the winter months on both the Pacific and Caribbean slopes of the country.

Elanoides forficatus yetapa. Swallow-tailed Kite. RV. We saw these kites frequently over the savanna but more often over broad-leafed forest. On 19 February 1962 I saw two birds, probably a pair, swooping over the tops of some tall pines as though foraging. Both alighted side by side in the top of a pine at least 35 m high, and I collected one bird, a female with some follicles enlarged to 3 mm. The stomach contained only a few chitinous fragments, apparently from crickets and spiders. I noted that powder down was abundantly dispersed through the plumage, imparting a grayish bloom to the dorsal surface, and that it was especially abundant (although not in discrete patches) on the rump; also, the uropygial gland seemed extremely small for a bird of this size. These data support suggestions that the fragmented down serves to waterproof the contour feathers in some falconiform species that inhabit regions of high rainfall (Beebe 1960). Colors of unfeathered parts were: iris, wine red; cere and base of bill, blue-gray; rest of bill, black; tarsi and toes light blue-gray, the toes with cream-colored undersurfaces.

Ictinia plumbea. Plumbeous Kite. Individuals sometimes perched or foraged among pines near the edge of broad-leafed forest. A male collected on 17 March 1966 at such an edge situation weighed 257, including a stomach packed with cicadas, and had testes measuring 12 × 7.

Buteo magnirostris direptor. Roadside Hawk. RV. These abundant hawks frequently range out into the savanna from the more favored broad-leafed forest edge. Data from specimens collected in such situations include: wts. two ad. ♂s, 247, 257 (latter with full stomach), and one ♀, 260; stomach contents from six birds: grasshoppers, cicadas, beetles, small snakes (2), small bird (1); gonad sizes: ad. ♀, 26 November 1966, largest follicles 1.5 mm; ad. ♀, 10 February 1962, two ruptured follicles; ad. ♂s: 19 January 1963, testes 7 × 5; 16 and 18 February 1962, 9 × 5; 21 March 1966, 12 × 6; im. ♂s (streaked pectoral plumage), 2 February 1962, 4 × 2; 18 February 1962, 7 × 3. I follow Monroe (1968) in not recognizing *arguta* as distinct.

Herpetotheres cachinnans cachinnans. Laughing Falcon. RV. This species perches in pines but usually not far from broad-leafed forest edge. A male taken in the savanna 18 April had testes 4.5 × 1.5; a female taken in rain forest 20 April, wt. 626, had no follicles larger than 1 mm. Both birds are in adult plumage with very worn rectrices, suggesting that nesting took place considerably earlier in the year.

Polyborus plancus audubonii. Crested Caracara. PR. Caracaras are present at all seasons in the savanna, but they tend to concentrate around villages and towns. A male collected 18 August 1965 had testes 8 × 3 and insect remains in the stomach. As pointed out by Griscom (1932:149), "In Central America the Caracara is abundant in the arid tropics and very rare or absent from the rain forest of the Caribbean slope." This species is unrecorded elsewhere on the Caribbean slope of Nicaragua, and although not recorded from the Honduran Mosquitia by Monroe (1968), it must occur there at least locally as I saw individuals opposite Waspam, on the north side of the Río Coco in Honduran territory, on 13 August 1965. The presence of caracaras in the high rainfall savanna region suggests that the species is adapted to habitats of generally open aspect and not specifically to the arid conditions in which such habitats are usually found in Central America.

Falco deiroleucus. Orange-breasted Falcon. The only one seen was a male collected 29 January 1962 from the top of a tall dead pine just outside an extensive area of rain forest at 40 km S of Waspam. The testes measured 10 × 6; colors of unfeathered parts were: iris, burnt umber; cere, base of bill, orbital skin, tarsi and toes, cadmium yellow. The bird was unwary, possibly because it had recently fed. The crop and stomach were both filled with meat, small bones, and a few feathers, and the stomach contained both feet of a small parrot, almost surely *Aratinga astec.* Slud (1964:73) also reports *A. astec* as prey of this species. Griscom's (1932:164) sight reports of *deiroleucus* nesting in belfries in Nicaragua and Panamá may apply to *F. rufigularis* as suggested by Wetmore (1965:282). Salvin and Godman (1901) cite one other record from Nicaragua (Matagalpa). Monroe's (1968) statement that I had observed this species "several times" is based on a misunderstanding, and I know of no other records from Nicaragua.

Falco femoralis femoralis. Aplomado Falcon. PR? This falcon is scarce but of regular occurrence in the savanna. The first one recorded had just made an unsuccessful swoop after a Plain-breasted Ground-Dove (*Columbina minuta*). The specimen records are: ad. ♂, 13 February 1962, testes 7 × 3; im. ♂, 3 February 1963, wt. 220, testes 5 × 3; ad. ♂ 25 January 1963, wt. 223, testes 5 × 4; colors of unfeathered parts: iris, burnt umber; base of bill, pale yellow-green, shading to deep blue-gray distally; cere, orbital skin, tarsi and toes, cadmium yellow; ad. ♀ 25 January 1963, wt. 332; largest follicles 4 mm. The latter two birds seemed to be a mated pair. All birds collected had empty stomachs. We saw a pair on 14 March 1966 and a single bird on 30 November 1966. The wide spread of dates of occurrence and the presence of a pair of which the female showed some enlargement of follicles suggest that there is a resident population in the Nicaraguan savanna, although Brown and Amadon (1968:825) consider the species to be only a migrant in Central America south of México. Measurements of the four Nicaraguan specimens are: 3 ♂s: wing, 229–236 (231); tail, 148–156 (152); ♀: wing 263, tail 173. These individuals approach the lower limit of the size range of the subspecies *femoralis* and cannot be considered migrants of the large northern form *septentrionalis.* Russell (1964) recorded the species in British Honduras in every month except January and July through October, and the single specimen available from that country is referable to *femoralis.* Thus, if not representing residents, the Nicaraguan savanna records and at least one British Honduras record would indicate extensive northward migration of some *femoralis* from South America during most of the year. The wing measurements (♂, 248; ♀, 279) given by Hellmayr and Conover (1949) for the only other Nicaraguan specimens, two immatures from the Pacific slope, are in the zone of size overlap of *femoralis* and *septentrionalis* and the specimens may not be identifiable subspecifically.

Falco sparverius nicaraguensis. American Kestrel. PR. I described this subspecies (Howell 1965) from

a series of 18 birds taken in 1962 and 1963; we obtained an additional three males and two females subsequently. The wing measurements and body weights of four of these birds are well within the size range of the type series, but one female taken on 26 March 1966 was unusually large. The wing measures 177.3, which extends the range of wing length by 0.7, and the weight of 134.5 is 46.9 heavier than any previously taken specimen. However, this bird had a full-size, incompletely-shelled egg in its oviduct and also a full stomach, both of which contributed to the unusually high weight. The stomach contents included an entire small lizard, identified as *Gymnophthalmus speciosus* by H. W. Campbell, and the tarsus and foot of a passerine bird that I identify as *Aimophila botterii*. Both specimens are preserved. Stomach contents of other kestrels included unidentified insect and lizard remains. Pertinent data on the other kestrel specimens are: 23 March, ♂, wt. 75.7 g, testes 5 × 4 mm; 26 March, ♂, wt. 73.2 g, testes 6 × 4 mm; 17 April, ♂, wt. unknown, testes 6 × ? mm; 11 March, ♀, wt. 84.5 g, 3 follicles 3 mm. The bird taken on 23 March is the first male of *nicaraguensis* to show a few tawny feathers in the otherwise all-gray crown; however, it is unusual also in having the back almost without any black markings and thus nearly uniform deep tawny.

We saw pairs copulating during March and as early as late January in 1962 and 1963. A male collected just after copulation on 23 January 1962 had testes measuring only 4 × 2.

Ortalis garrula cinereiceps. Rufous-winged Chachalaca. Although not a visitor to the savanna proper, these cracids may be found in narrow streamside borders and "islands" of broad-leafed vegetation throughout the savanna. A male collected at Leicus Creek 25 November had the crop packed with large pieces of fresh, dark-green leaves, apparently all of the same kind; the stomach contained some leaf matter and seeds. This chachalaca almost certainly ranges north into nearby Honduras although it is presently known from that country only in the Olancho region (Monroe 1968). Wetmore (1965) regards *cinereiceps* as specifically distinct from *garrula*.

Colinus nigrogularis segoviensis. Black-throated Bobwhite. PR. This quail reaches the southern limit of its range in this part of Nicaragua. It is confined to the pine savanna and is common wherever ground cover is not too sparse. Monroe (1968) considers *segoviensis* Ridgway a valid subspecies, restricted to the Mosquitia of Honduras and Nicaragua. I have not examined a series of more northern populations, but the measurements of my series of eight adult males and four adult females support Monroe's conclusion that the Mosquitia population represents a small form. As the primaries of these quail are considerably curved there is a difference of several millimeters between measurements of the chord and of the flattened wing, as follows: 8 ♂: chord: 86.4–91.1, $\bar{x}$ = 89.0; flattened: 89.7–95.1; $\bar{x}$ = 92.7 and for 4 ♀: chord: 87.8–92.0, $\bar{x}$ = 90.7; flattened: 91.2–95.7, $\bar{x}$ = 93.9. Monroe's figure $\bar{x}$ = 93.5 for males of *segoviensis* refers to the flattened wing.

In color, the series of adult males is quite uniform dorsally, but the extent and degree of black emargination of most of the ventral plumage are highly variable and range from heavy to sparse. Extremes are represented by: (1) a male taken on 26 August 1965 in which the basically white feathers of the breast, upper abdomen, and flanks are broadly margined and speckled with black, the black margins largely masking the usually chestnut borders of the flank feathers; (2) a male taken 29 January 1962 in which the feathers of these same regions are broadly margined with chestnut, black being confined to narrow margins in the lower breast and upper abdomen and some small subterminal splotches along the flanks. The six other adult males are intermediate between these extremes although five are closer to type (1) and one is closer to type (2). Possibly a larger series would indicate that there are two color phases. The differences do not seem to be correlated with age as an immature male still showing some juvenile feathers, taken 26 August 1965, has more blackish margining than the adults of type (2) above. The four adult females do not show a comparable degree of variation. Weights recorded were: 2 ad. ♂, 111.7 and 114; 1 ad. ♀, 120.7; 1 im. ♂ (26 August), 94.4; 1 juv. ♂ and 4 juv. ♀, collected from the same covey on 18 August 1965, 71.7, 74.3, 74.7, 75.2, 75.7, respectively. Some adult males had enlarged testes during each month that they were collected; the sizes ranged from 2 × 2 to 8 × 5 on 29 and 30 January 1962; 4 × 3 to 10 × 7 to 12 × 7 in March and April; 8 × 4 on 26 August. The only females were obtained in late January and early February, and only the one taken on 4 February 1955 had definitely enlarged follicles, up to 3 mm. The five juveniles had attained roughly 65% of adult weight, and if their growth rate was similar to that recorded by Roseberry and Klimstra (1971:118) for *C. virginianus*, their post-hatching age would be about 60 days, which would put the time of hatching in the fourth week of June. By the same rough calculation, the 94.4-g immature may have been hatched in early June. These two nestings would thus have been initiated after the beginning of the wet season. From November into February the quail were found in coveys, usually of 10 to 12 birds; in March and April they were usually in pairs. The "bob-white" song, identical with that of *C. virginianus*, was heard at all seasons.

On 14 March 1966 a male and three females were encountered in a semi-open patch of ground; I made squeaking sounds, and the male advanced toward me to within 0.5 m with drooping, half-spread wings and much-ruffled body plumage; one female followed in a similar pose while the others remained about 1 to 2 m away. My slow movements did not panic the birds, and the male led them away calmly. The behavior seemed remarkably bold and suggested a high level of aggression.

Laterallus ruber. Ruddy Crake. WrR. This rail is probably widespread in marshy areas in the savanna and we often heard its calls in such places. The only specimen obtained is a male taken 23 November 1966, wt. 46.2, testes 4 × 3; the stomach contained grit and small seeds.

Columba cayennensis pallidicrissa. Pale-vented Pigeon. RV. These pigeons often fly over the savanna or perch in the tops of dead pines. Sometimes they were flushed from clumps of mistletoe, *Psittacanthus mayanus*, in pines, and presumably they eat the berries of this plant. The three-note call is distinctive and has a hooting quality. I noted the display flight behavior, as described by Wetmore (1968:9), in March and April. On 23 April 1967 we found two nests, both on the ground at the bases of palmetto clumps near ponds in the savanna. One contained a single, pure white egg, and the other contained a

TABLE 1. Measurements for *Amazona ochrocephala parvipes*.

Date	Sex	Wing	Tail	Wt.	Gonad size
26 November 1966	♂	203.2	106.7	445.5 (fat)	testes 9 × 2.5
26 November 1966	♀	193.2	103.2	435.3 (fat)	largest follicle 2 mm
26 March 1966	♀	205	107.2	440.2	largest follicles 5 mm
30 January 1963	♂			446.0 (slightly fat)	14 × 5
26 January 1963	♀			391.7	largest follicles 3 mm
27 January 1963	♀			397.3	largest follicles 3 mm
29 January 1963	♀			402.5	largest follicles 2.5 mm
3 February 1962	♀				largest follicles 3.5 mm
3 February 1962	♂				left, 17 × 5, rt, 10 × 4

single squab 8 or 9 cm in length, with only down feathers along the pterylae. Both nests were formed out of the grasses in which they were located, without sticks or other materials. Data from specimens are: ♀, 28 January 1962, two largest follicles 6 mm, several others 3 mm; ♂, 17 March, wt. 258.8, crop filled with berries; testes 12 × 8; ♂, 13 March, wt. 233.3, testes 18 × 10.

Columba speciosa. Scaled Pigeon. RV. This larger species visits the savanna less often than the preceding one and appears to use the habitat in a similar way, but we found no nests. A juvenal male taken at the savanna edge on 22 August weighed 261.8, had berries of *Byrsonima crassifolia* in its crop, and had testes 6.5 × 2.5.

Columbina minuta interrupta. Plain-breasted Ground-Dove. PR. A small population of these doves was found at about 25 miles NW of Puerto Cabezas, and they were not encountered elsewhere. A male that was missed by an Aplomado Falcon (see above) was collected on 13 February 1962. The data from the only two specimens are: ♂, testes 10 × 5; bill, dark umber; iris, purplish gray; tarsi and toes, flesh color; ♀, 1 February 1963, wt. 33.5, largest follicles 1.5 mm; bill, olive; iris, light cream; tarsi and toes, flesh color (Buchanan notes). We saw two pairs at this same locality at the time the single female was collected. There are no previous published records of this species from Nicaragua, and my only other record is of a pair taken in the Depto. de Nueva Segovia in the north central highlands. The species appears to be very locally distributed, but it could easily be overlooked or not distinguished from two similar congeneric forms. *C. passerina* is numerous in the town of Puerto Cabezas and its outskirts, but was not found anywhere in the pine savanna. *C. talpacoti* was not recorded in the savanna either although it is abundant elsewhere in both the Caribbean and Pacific lowlands.

Ara ambigua. *Great Green Macaw. We saw a group of six birds over the savanna in the early morning on 3 February 1962, and in 1966 and 1967 we noted groups of Great Green Macaws in the adjacent broad-leafed forest. The calls of this species are noticeably louder than those of *A. macao*.

Ara macao. Scarlet Macaw. RV. On 11 March 1966, a pair of macaws flew into an area of pines in which I conducted regular censuses and alighted in a large dead pine, where they kept up a noisy dialogue of squawks while looking into cavities in the tree as though prospecting for a nest site. They flew off as another noisy pair of macaws came over, but later in the day I again saw two birds alight in the same group of pines. This was the same place frequented by a pair of *Amazona ochrocephala* and both species appeared to be nest-site prospecting there although not simultaneously. No evidence of actual nesting by either species was found in March 1966, but in April 1967 a pair of macaws was regularly present at this spot. In a large pine from which the top had broken off, a deep cleft had formed at the breaking point and the macaws appeared to have chosen this as a nest site. One or two macaws occupied this tree every day, often looking into the cleft, and they allowed us to approach closely in contrast to the extreme wariness of this species in neighboring areas. I obtained color motion pictures on 28 April, 2 days before our departure, but we did not attempt to climb to the site for fear of causing desertion and the fate of the presumed nesting attempt is unknown.

One macaw was collected at Leicus Creek on 29 January 1963 as it flew along the forest edge-pine savanna interface.

Amazona ochrocephala parvipes. Yellow-headed Parrot. PR. Subsequent to the description of this subspecies (Monroe and Howell 1966), we collected another male and two females in the Nicaraguan savanna near the type locality. All three have yellow napes and exhibit the other color characters ascribed to *parvipes*; middle toe and culmen-from-nostril measurements are well within the size range of the type series, but the wing (chord) and tail measurements are virtually equal to or smaller than the lowest extremes previously reported. Data on these three specimens and previously unpublished data on Nicaraguan birds in the type series are shown in table 1.

The two collected on 26 November were a pair. The remiges and rectrices of all three 1966 birds show only slight wear. If anything, the measurements of the chord of the wing are slightly longer than the true chord, as I flattened the wing slightly in exposing fully the longest primary.

Although we often saw pairs in pines with suitable-appearing holes, we found no nests.

Bubo virginianus. *Great Horned Owl. PR? There are two sight records, each of a single bird, from a pine savanna census area at Leicus Creek. On 1 December 1966 an owl flushed from a large pine shortly after sunrise and it flew out of sight into dense broad-leafed forest several hundred meters away. On 23 April 1967 Stiles flushed an owl from an apparent roosting place on the ground in the same study area, again shortly after sunrise. Both Stiles and I then saw the owl perched in a pine, but when we tried to approach closer it flew off for at least 1 km and was lost to sight. Attempts to relocate the bird on both occasions and many attempts to find owls in the pines

TABLE 2. Measurements of *Chordeiles minor* from the Nicaraguan pine savanna, and those of subspecies breeding in Central America and southeastern United States (Eisenmann 1962).

Date	Sex	Age	Wing	Tail	Wt	Gonad size; fat condition
22 Aug	♂	ad	183.5	>94.3[a]	67.0	— slightly fat
27 Aug	♂	ad	174.5	91.8	58.0	2 × 1; slightly fat
23 April	♂	ad	174.1	96.6	64.8	— —
28 April	♂	ad	180.6	91.1	60.0	8 × 7; no fat
			$\bar{x}$ = 178.2	>93.5		
25 Aug	♂	1st year	171[b]	91.8	71.7	1; slightly fat
18 April	♂	1st year	184.6	98.4	60.4	7 × 4; no fat
23 April	♂	1st year	184.2	96.3	67.1	10; no fat
29 July	♂	1st year	181.8	>94.6	—	— —
			$\bar{x}$ = 180.4	>95.3		
25 Aug	♀		174.0	90.7	63.7	follicles <1; no fat
22 April	♀		173.2	96.2	76.6	largest follicles 3, 7; slightly fat
19 April	♀		185.0	100.1	66.4 (body) 14.0 (stomach)	largest follicle 4.5; no fat
			$\bar{x}$ = 177.4	95.7		

[a] minimal length; feathers broken
[b] extrapolated; tips of longest primaries broken

n	Sp.	Sex	Age	Wing	Tail
6	*neotropicalis*	♂	ad	188 –199 (195.3)	103–112 (106.8)
2	"	♀	ad	178 –187 (182.5)	95– 96 (95.5)
1	*panamensis*	♂	ad	187	99
4	"	♀	ad	175 –185 (181)	96– 97 (96.5)
10	*chapmani*	♂	ad	178 –192 (184.1)	99–110.5 (105)
10	"	♀	ad	172.5–184.5 (179.4)	99–108.5 (103.2)

at night were unsuccessful; no calls were ever heard. I suspect that the Great Horned Owl is a rare resident of the pine savanna but have no evidence in addition to that cited above.

Glaucidium brasilianum ridgwayi. Ferruginous Pygmy Owl. RV. On 2 February 1955 two of these owls were collected about 25 m apart—a male in the grayish brown phase (Group 1; Dickey and van Rossem 1938) at the edge of a broad-leafed thicket, and a female of the ferruginous phase (Group 3) in pines. Neither had enlarged gonads. On 23 January 1962 a female of the ferruginous phase was collected in a broad-leafed thicket along a stream running through the pine savanna; the follicles were not enlarged. There is no indication that these owls venture far into the pines away from broad-leafed vegetation although no other small owls range into the savanna.

Nyctibius griseus costaricensis. Common Potoo. RV. Potoos sometimes come out of the broad-leafed forest into the pines at night, but we never found them there during the day. We never heard the calls of this species in the savanna, and the three birds obtained were located by the brilliant eye shine: ♂, 6 February 1962; testes 11 × 8; ♂, 10 February 1962; testes 8 × 5; iris yellow-orange; ♂, 26 April 1967; testes 5 × 4; wt. 241; stomach full of insect fragments.

The uropygial gland is minute, but this species has, on each side of the rump, a patch of grayish powder-down about 25 mm in diameter. The powder-down is presumably used as a water-repelling agent.

Chordeiles minor. Common Nighthawk. SR. This species was not recorded during the November, January, February, and March visits, but was abundant during April and August. We found no nests but have strong presumptive evidence of breeding. In August we frequently saw nighthawk caracasses, many of them juvenals, along the roads in the savanna. Most could not be saved, but I made a skin of one picked up on 12 August. The gonads were not detectable, but the plumage is that of a juvenile female with the primaries incompletely grown and still ensheathed at their bases. There was no subcutaneous fat. We saw no nighthawks in March up to our departure date of 26 March 1966, but on our arrival in the savanna on 16 April 1967, they were abundant and frequently gave booming displays. Four males and three females were collected in April and all had enlarged gonads (table 1); one female, taken on 22 April, had two enlarged follicles measuring 3 and 7 mm in diameter. These data leave little doubt that a breeding population was present. A specimen in the Royal Ontario Museum (ROM 25827), a male taken on 29 July 1905 by M. G. Palmer at San Ramón, Río Wanks (= Río Coco), "about 185 miles above Cape Gracias" (a Díos) is a further indication of summer residence.

The subspecific allocation of this population is problematical. *C. minor* breeds locally in suitable habitats in Central America from México to Panamá (Selander and Alvarez del Toro 1955; Eisenmann 1962, 1963; Russell 1964; Monroe 1968) and I have compared the Nicaraguan series of eight males and four females with one example of *neotropicalis*, with Russell's birds from British Honduras, with the five specimens of *panamensis* available in 1968, and with a large series of *chapmani* from southeastern United States. Wing and tail measurements for the nonjuvenile Nicaraguan specimens and other relevant data are given in table 2. Measurements of *chap-*

TABLE 3. Measurements of *Caprimulgus maculicaudus*.

Locality	Sex	n	Wing ($\bar{x}$)	n	Tail ($\bar{x}$)
México	♂	14	127 –138.2 (131.5)	14	97.0–111.7 (101.6)
	♀	13	126.7–135.3 (130.7)	11	88.7– 99.8 (95.0)
Honduras	♀	2	127.5–129.3 (128.4)	2	94.9– 97.3 (96.1)
Nicaragua	♂	6	122.6–132.4 (128.2)	6	93.5– 99.2 (95.5)
	♀	4	120.6–126.7 (123.9)	4	85.0– 91.3 (88.5)
NW Colombia	♂	7	128.2–136.2 (133.6)	8	96.6–104.6 (100.3)
	♀	2	128.4–134 (131.2)	2	90.0– 98.0 (94)
E. Colombia	♀	3	127.5–130 (129.0)	3	92.5– 98.2 (95.4)
Guyana; French Guiana	♀	4	124.4–132.4 (128.4)	3	89.5– 99.5 (93.5)
Brazil	♂	16	126.4–136.0 (131.8)	13	96.4–106.2 (101.1)
	♀	9	120.0–129.3 (124.8)	9	88.4– 94.5 (91.8)
Bolivia	♀	2	133.2 (133.2)	2	94.1– 94.5 (94.3)

mani, *panamensis*, and *neotropicalis* are quoted from Eisenmann (1962).

All but one of the Nicaraguan birds have wing and tail measurements less than the lower extremes recorded for *neotropicalis* and thus with one possible exception do not represent that form. In size most of the Nicaraguan birds are comparable to *panamensis* and *chapmani*, but none resembles *panamensis* in color as all lack the rufous and tawny tone of the mottling on the dorsum, secondaries, and wing coverts of that form. In fact, the Nicaraguan birds are indistinguishable from *chapmani* in coloration except for the position of the white wing bar. When the wings of study skins of adults of both forms are lined up evenly, the white bar in Nicaraguan birds is more posterior; its anterior border lies opposite the posterior half of the bar in *chapmani*. Tail length in Nicaraguan birds also averages shorter than in *chapmani*.

It seems highly probable that a subspecifically distinct population of small-sized nighthawks breeds in the pine savanna, but a formal description would be premature. The first-year birds, taken in April, average larger than the adults, and it is possible that a few of the Nicaraguan specimens are migrants of *chapmani* or even of *minor* or *neotropicalis*. A larger series of birds known to be breeding in the savanna is needed, as well as further collecting of breeding nighthawks in the region between Nicaragua and southern México.

The Lesser Nighthawk, *C. acutipennis*, has not been recorded from the pine savanna.

Caprimulgus maculicaudus. Spot-tailed Nightjar. SR. I first detected this species on 22 March 1966 when a male giving the distinctive "pit-sweet" call was collected shortly before dawn in open, grassy savanna with a few scattered pines. We obtained three others at the same spot on 25 March, but in November 1966 we found none despite intensive searching in the early evening and predawn hours. In April 1967, we heard and collected nightjars at the same and at similar localities in the savanna. All specimens had enlarged gonads. A female with a yolked follicle 13 mm in diameter was taken on 22 April and one with a shelled egg in the oviduct was obtained on 23 April, which definitely establishes breeding in the savanna. It is possible that these birds are permanently resident and that we failed to find them in other months as they were not calling, but I think it probable that we would have found them by eye-shining and that they migrate away for the winter.

On 25 March, at least three males were calling in an area about 5 acres in extent. They began calling shortly after dark, and the birds foraged in flight less than 2 m above the ground, frequently alighting on fallen logs or short stumps. The coarse grass was about 0.5 m high in this area. On 26 March, I collected a pair about 15 min after dark, and although they could not have been foraging for much longer than that time interval, the stomachs of both were crammed with a single species of scarabaeid beetle. The female had 23 in its stomach and two more in the mouth and esophagus; the male had 25 in its stomach. Both stomachs were so distended as to be translucent, and the dark markings of the beetles could be seen through them. These data suggest that 25 such beetles, a total weight of 5 g, is a maximum food intake during early evening feeding. Other stomach contents recorded were small click beetles (Elateridae), a wasp, and moths.

With a series of six males and four females from Nicaragua, I assembled a comparative series of most specimens of this species in American museums from México and Honduras (the only other known Central American localities) and from Colombia, Bolivia, Guyana, and Brazil. These included almost all of those examined by Blake (1949) and many more collected subsequently. My measurements (table 3) differ slightly from Blake's but support his conclusion that no subspecies should be recognized. Mean size decreases from México to Nicaragua and birds from the latter region are the smallest, but those from northern South America are larger and statistically indistinguishable from Mexican populations. Sexual dimorphism in size is greatest in the Nicaraguan and Brazilian series, with females in the latter population approaching the small size of those in the former. I find no consistent color differences over the entire range except that most birds in a series from along the Amazon in the state of Pará, Brazil, are grayer and less rufescent than any others. As Blake noted, all but one of 21 such birds are from Santarem and nearby Obidos; there may be partly localized gray and rufous color phases in that region. As widely separated populations are indistinguishable from one another and as the samples from some localities are small, recognition of subspecies is presently unwarranted.

Amazilia cyanocephala chlorostephana. Red-billed Azurecrown. PR. We obtained three males and one female subsequent to the collection of the type series (Howell 1965). The female is an immature bird ob-

tained on 24 August; it has grayish tips to the rump feathers and a less glittering crown than that of definitive adults. This bird weighed 4.9 and the weights of three males were 4.5, 5.2, and 6.4. In the pines these hummingbirds forage while hovering around clusters of pine needles, before bark crevices, and at the red flowers of *Psittacanthus mayanus* and the bromeliad *Aechmea bracteata*.

Piculus rubiginosus yucatanicus. Golden-olive Woodpecker. RV. Wing measurements of three males (119.8, 120.0, 120.2) and one female (117.3) are in close agreement with Monroe's (1968:209) figures from the Honduran Mosquitia, and all are within the size range of *yucatanicus*. All the specimens from the pine savanna area appear darker and less golden-olive ventrally than most of those from other areas, but there is much individual variation and birds from any region can be matched in color by individuals from another. The darker appearance is caused by a reduction in the suffusion of golden-olive color, which is primarily localized on the rachis and barbs, not on the barbules. It is possible that foraging over rough pine bark wears away this "gloss" without necessarily causing a heavily abraded appearance. However, microscopic examination shows that the feathers of pine savanna birds are comparatively less golden-olive even on the basal parts that are shielded from abrasion, and wear cannot account altogether for the color differences.

These birds often venture out into the pines from the adjacent broad-leafed forest, but they are not found far out in the savanna and we found no nests in pines. Birds were heard drumming as early as 29 January, and males collected on 5 February and 17 April had testes measuring 5 × 3 and 7 × 3, respectively. A female taken on 25 November did not have enlarged follicles and weighed 80.2.

Dryocopus lineatus similis. Lineated Woodpecker. RV. Like the preceding species, this one ranges out into the pines from the adjacent broad-leafed forest. Although we found no nests, many large holes in dead pines may be the work of this woodpecker and these may provide roosting and nesting sites for birds such as parrots and kestrels.

Melanerpes formicivorus albeolus. Acorn Woodpecker. RV. These woodpeckers are closely associated with oaks (*Quercus oleoides*) and are frequent visitors to the pines only in the vicinity of oaks. Dickey and van Rossem (1937) commented that no acorn storage was seen in El Salvador populations of this species, but the Nicaraguan birds store acorns in abundance in both oaks and pines. Visits to the pines were often associated with this activity, and in virtually every respect the behavior and vocalizations of these birds seemed identical to more northern populations. On 1 December, I saw two birds fly out of the oaks to an epiphyte about 15 m up in a tall pine, where they probed among the bases of the epiphyte leaf cluster. These epiphytes often support colonies of ants and also hold water, and the woodpeckers may use both resources.

Four males and five females were collected during the first half of February in 1955 and in 1962. Testes size ranged from 3 × 3 to 8 × 5, but follicles were not enlarged beyond 1.5 mm and no birds had incubation patches. An additional male taken on 18 April weighed 85.2, had testes measuring 6 × 4, and had a well-developed incubation patch.

When Todd (1910) described *M. f. albeolus* from British Honduras, he compared his series only with examples of *striatipectus* and *formicivorus*; as he stated, the sides and flanks are less streaked and the throat paler yellow than in the former, and the pectoral band is more striated, less solid black, than in the latter. Dickey and van Rossem (1927) also compared their type series of *M. f. lineatus* only with examples of *striatipectus*, *formicivorus*, and several more northern forms, stating that they had not seen ". . . *albeola* Todd, but the characters ascribed to that form would seem to make direct comparison unnecessary." On the contrary, direct comparison shows that the two forms are extremely similar. I have compared the Nicaraguan savanna series with others from the Nicaraguan highlands, van Rossem's series from El Salvador, four from the Honduran highlands, two from the Honduran Mosquitia, and 10 from British Honduras. As mentioned by Monroe (1968), I cannot distinguish any of the Nicaraguan savanna birds from the *lineatus* series from El Salvador. However, Monroe's two specimens from the Mosquitia have less heavy pectoral streaking and resemble closely some specimens from British Honduras. Of the latter birds, two have distinctly narrower central shaft streaks in the pectoral band, and these and six others appear less heavily black in the anterior part of the band; the remaining two have the pectoral band as in *lineatus*. The throat averages slightly paler than in *lineatus*, but there is much overlap through individual variation.

Excluding badly worn birds, I obtained the following wing measurements: El Salvador, 5 ♂, 141.5–143.3 (142.8) and 9 ♀, 130.7 (*sic*)–144.5 (139.6); Nicaragua and Honduras highlands, 4 ♂, 133.0–143.4 (139.1) and 1 ♀, 140.5; Nicaraguan savanna, 5 ♂, 138.5–144.9 (141.0) and 5 ♀, 140.0–145.4 (142.7); Honduran Mosquitia, 1 ♂, 137.6 and 1 ♀, 135.1; British Honduras, 2 ♂, 137.1–142.0 (139.5) and 5 ♀, 133.1–145.9 (138.5). I have not included Ridgway's (1914) measurements, which must have been made on Todd's series of "very worn material" (Griscom 1932:225).

Although the British Honduras and Honduran Mosquitia birds average slightly smaller than those from the Nicaraguan savanna and El Salvador, no statistical analysis is needed to see that the difference is not significant.

I conclude that there is a trend toward lighter pectoral streaking and slightly shorter wing length in British Honduras and at least some Honduran Mosquitia birds as opposed to those from the interior highlands and the Nicaraguan savanna, but these differences are not pronounced and consistent enough to support recognition of two subspecies. I think that the Caribbean lowland populations are a relatively recent derivative of the highland birds, but *albeolus* is the older name and *lineatus* becomes a synonym.

Sphyrapicus varius varius. Yellow-bellied Sapsucker. WR. Sapsuckers were scarce in the pines and even scarcer in the broad-leafed forest edge. We found their characteristic rows of holes in large examples of *Curatella americana* in the savanna, but most birds seen were in pines. We saw none in August or April, but found them from 25 November to 18 March. Two females collected on 31 January 1963 weighed 47.5 and 42.0 and are in first year immature plumage (= first basic), with only a few black feathers showing in the pectoral region. All others seen closely enough to tell the sex, a total of at least five, were also females.

The remiges and rectrices of both specimens are relatively unworn and measure as follows: wing, 123.4, 120.7; tail, 73.4, 71.5. The measurements are within the zone of overlap of *S. v. varius* and *S. v. appalachiensis* and the immature plumage is not diagnostic, but the probability is that they represent *S. v. varius*. The validity of *appalachiensis* should be checked by adequate statistical analysis of the apparent size differences.

Dendrocopos scalaris leucoptilurus. Ladder-backed Woodpecker. PR. Unlike the previously listed picids, these small woodpeckers are not visitors to the pine savanna but are strictly confined to that habitat. They are nevertheless scarce and irregularly distributed throughout the savanna, a puzzling fact in view of the apparent absence of potential competitors. Ladder-backs are usually solitary except during the breeding season, which extends at least from mid-March through April but has not commenced by early February. Relevant measurements from a series of 12 birds are as follows: 3 ♂, wt. 24.8–27.4 (26.1), wing 84.8–86.2 (85.7), tail 46.3–48.3 (47.2), culmen from nostril 14.4–14.9 (14.6); and 8 ♀, wt. 23.0–26.5 (24.7); 9 ♀, wing 82.5–85.8 (84.1), tail 45.0–49.4 (47.0); 6 ♀, culmen from nostril 12.2–13.3 (12.8). (Only wing and tail measurements available for all 9 females.)

The data show that sexual dimorphism in size is greatest in bill length, which presumably diminishes competition between the sexes for some kinds of food. In size and in color, the Nicaraguan population is not distinguishable from *leucoptilurus*, the very small-sized subspecies found in Honduras and British Honduras. As is the case with several other pine savanna birds, this species is primarily an inhabitant of arid regions in other parts of its range and reaches its southern limit in the Nicaraguan pine savanna. Its distribution becomes increasingly patchy south of México and it has not been recorded elsewhere in Nicaragua or in El Salvador despite an abundance of apparently suitable arid habitat.

These birds tend to move rapidly through the pines, flaking bark off small branches as they spiral around them toward the tip, often probing and gleaning among cones and at the bases of small bromeliads (*Tillandsia*). Even when not alarmed, they may fly for long distances before alighting. These habits and the birds' scarcity suggest that food is scarce and that foraging over a large area is necessary, as is often true in arid habitats also.

A pair collected on 14 March behaved as though near a nest site, and both birds had well-developed incubation patches and enlarged gonads. Another pair collected on 25 April was in similar reproductive condition. On 17 April, a male was seen and heard drumming on small dead pine. Shortly after this bird departed, a female was collected nearby after she drummed once in a nearby pine in response to drumming of an unseen bird in the distance. This female had a partly developed incubation patch and the largest follicle measured 1.5 mm.

Pyrocephalus rubinus pinicola. Vermilion Flycatcher. PR. We obtained six males and three females since collection of the type series (Howell 1965), and I have examined a previously unreported pair (ROM 6476, 6478) taken 24 February 1905 by M. G. Palmer at "Sacklin, Rio Wanks (= Río Coco), 50 miles below Cape Gracias" (a Díos). Measurements of this additional series show that *pinicola* averages very slightly larger than previously reported; the new figures are: 16 ♂, wing 69.5–72.4 (71.1); 17 ♂, tail 49.3–55.0 (51.9); 7 ♂, wt. 13.0–15.6 (14.3); and 11 ♀, wing 65.4–70.6 (68.3); 10 ♀, tail 48.5–54.1 (51.1); 4 ♀, wt. 12.0–16.1 (14.5).

In color, the additional females show the broad, blurred pectoral streaking and the infusion of red anteriorly into the pectoral region as originally ascribed to *pinicola*. Two females taken 22 March and 20 April show slightly less red on the abdomen and are slightly more pinkish, less orange, than others in the series. A male with a double-layered skull taken 27 August has the remiges and rectrices in molt.

On 21 January 1963, I saw two males perched in the tops of small pines about 20 m apart. One male made several circling flights about halfway to the other male. The wings of the flying bird made a very audible whirr, as described by Smith (1967). The second male remained perched. I collected the apparently aggressive bird, which had slightly enlarged testes measuring 2.5 × 2.

On 14, 15, and 18 March, we noted display flights of males as they fluttered up, stalled, and glided down (Smith 1967), but we did not record details. One displaying male and its apparent mate were collected on 14 March; the male had asymmetrically enlarged testes measuring 9 × 4 and 3 × 3, and its mate had follicles less than 1 mm in diameter. Two days later another male was displaying in the same place where this pair was collected. On 18 April, I saw courtship feeding in a nesting pair. A male flew down to the ground, picked up a large insect, and returned to a pine. A female flew over, alighted about 7 m up in another pine, and the male flew over to her. The female crouched, fluttered her wings slightly, and raised her bill in a begging posture. The male several times took wing and hovered in front and slightly to one or the other side of her, thrusting the insect into her open bill. Unfortunately, I was not able to see if the female got all or part of the insect or whether the male finally swallowed it. About 10 min later, the female flew to an incomplete nest straddling a branch about 6 m up in a small pine. She settled on the nest for a few moments, tucked in some material, and left. On 25 April, I found a nest containing young; it was saddled on the fork of a small branch about 10 m high in a large solitary pine tree. Several times, the female flew out of the nest tree, hovered at the level of the highest grass stalks (about 0.5 m), then dropped into the grass to seize an insect and returned to the nest. As I approached, both male and female showed agitation and flew over close to the nest. A female collected on 20 April had a well-developed incubation patch, and three males collected on 17, 22, and 25 April had testes sizes from 6 × 4 to 8 × 4 but no incubation patches.

Muscivora savana monachus. Fork-tailed Flycatcher. PR. We recorded Fork-tails as common at all seasons but irregularly distributed in the savanna. They usually occur in open grassy areas, often in loose flocks of 10–12 birds, resting on low shrubs or tall grasses and feeding near or on the ground. On 25 January 1962, I saw one eating small berries in a low tree at the edge of the savanna. We noted pairs as well as flocks in March, but the male of a pair collected on 13 March showed only moderate testes enlargement (5 × 3) and there was virtually no follicle enlargement in the female. In mid-April 1967, most birds were paired. Males collected on 17, 18, and 22 April had testes sizes ranging from 11 × 5 to 14 × 7, and a female taken on 20 April had an un-

shelled egg in its oviduct. This bird had a well-developed incubation patch, and a male taken on 22 April had a moderately developed incubation patch—a condition not detected in two other April-taken males. On 20 April, I saw a Fork-tail persistently chasing a male Vermilion Flycatcher around through a grove of small pines in an area where both species were paired and showed territorial behavior.

Weights of specimens were: 4 ♂, 26.7–31.0 (28.8); 2 ♀, 26.6, 35.0 (with egg in oviduct).

The Scissor-tailed Flycatcher (*M. forficata*) has not been found on the Caribbean slope of Nicaragua although it is an extremely abundant winter resident on the more arid Pacific slope of the country. Evidently most of the south-bound migrant Scissor-tails are concentrated on the Pacific slope by the time they reach Guatemala, and the last of those still moving along the Caribbean slope cross to the Pacific side through Honduras and do not reach the pine savanna.

Smith (1966) considers *Muscivora* a subgenus of *Tyrannus*. He gives an excellent summary of the morphological and behavioral characteristics by which the two *Muscivora* species are "adapted to a habitat that is unusually open for kingbirds" and points out that these two species are the only ones broadly sympatric with other species included in *Tyrannus*. However, he maintains that the "structural, plumage, and behavioral similarities between *Tyrannus* and *Muscivora* are extensive, and our classification would do better to recognize these than to recognize the ecologically oriented differences." If one test of a genus is that its members exemplify a new adaptive direction or departure from that shown by closely related species, then *Muscivora* seems worthy of continued recognition. As Smith points out, the relatively small body size and greatly elongated rectrices appear to be adaptations for hovering at very low levels, which permits effective foraging in open situations just above the vegetation and on patches of open ground. Thus, the *Muscivora* species can exploit resources not readily available to *Tyrannus* species and can exist sympatrically with the latter. The two *Muscivora* species, on the other hand, are not sympatric as breeding forms and, as pointed out above and by Slud (1964), the two species are largely or entirely allopatric over most of their winter ranges although *forficata* migrates through some of the range of *tyrannus*. I therefore prefer to retain *Muscivora* while admitting its close relationship to *Tyrannus*.

Tyrannus melancholicus chloronotus. Tropical Kingbird. RV. Kingbirds often came out into the pines from the broad-leafed forest edge but seldom very far, and they did not appear to be colonizing the pines or losing their association with their typical habitat. They were usually paired and actively territorial in April, and a male collected on 23 April weighed 47 and had testes measuring 16 × 8. This bird also had an incubation patch although the male of this species is not known to incubate or brood (Skutch 1960). A male taken on 20 November weighed 40.1 (slightly fat), had unenlarged testes, and had five scarabaeid beetles, each about 6 mm long, in its stomach.

Elainea flavogaster. Yellow-bellied Elainea. RV. This species is also an inhabitant of edges and clearings but may range out into the pine savanna. This was particularly noticeable in March and April, when we found pairs consistently in the same areas of pines and noted much noisy aggressive behavior, presumably territorial. No nests were found, but it is possible that this species sometimes nests in the pines. A male collected on 13 February 1962 had testes enlarged to 8 × 5, and a male taken on 13 March 1966 weighed 28.1 and had testes measuring 10 × 5.

Brodkorb (1943) discussed variation in the Central American populations of this species. He pointed out that the type of *subpagana* came from Dueñas, Guatemala, on the Pacific slope and assigned the name to populations of the Pacific lowlands from southeastern Chiapas to El Salvador and possibly to Nicaragua. These he characterized as paler and grayer dorsally, paler and less brownish on the throat and chest, and paler yellow on the belly as compared to Gulf and Caribbean lowland populations from Veracruz through Nicaragua and to southwest Costa Rica and Chiriquí on the Pacific side. He described the humid lowland populations as *saturata*, darkest of the subspecies.

I previously assigned birds from Caribbean Nicaragua (Howell 1957) to *saturata* as they appeared to differ by their darker coloration from a small series of birds—four from El Salvador and one from Aranjuez, Puntarenas, Costa Rica—that should represent *subpagana*. *E. flavogaster* is a scarce bird in the arid Pacific lowlands south of Guatemala; van Rossem cited only five specimens from El Salvador, and Monroe (1968) lists only one locality (San Francisco, Choluteca) in the Pacific lowlands of Honduras where specimens were obtained. I have none from the Pacific slope of Nicaragua, and it is apparently rare in the dry northwest quadrant of Costa Rica (Slud 1964). Neither Russell (1964) nor Monroe (1968) recognizes *saturata*, and I re-examined the series from El Salvador and Costa Rica and compared these with eight specimens from Caribbean Nicaragua. The color differences described by Brodkorb are apparent to me, but unfortunately, the *subpagana* specimens are rather worn and this may be responsible for their paler tones. Brodkorb also stated that *subpagana* has a heavier, shorter, and wider bill, but I am unable to see this. I think that *saturata* and *subpagana* may be distinct, but this can only be determined by comparison using a freshly plumaged series of unquestionable *subpagana*, which may be a rather scarce subspecies with a narrow range along the Pacific lowlands.

Progne subis subis. Purple Martin. M. Extreme dates of early occurrence of this fall and spring migrant are 19 August 1965 and 1 February 1963 (both collected). The adult males are readily distinguishable from the resident *P. chalybea*, and sight records pertain only to males or to groups of both sexes. We saw individuals several times in mid-March and found a flock of about 65 perched in a dead tree in the savanna on 21 March. I estimated that two-fifths of these were adult males. None was recorded in April. The adult male collected on 1 February weighed 45.9 and had enlarged testes measuring 4 × 2.5. Another adult male collected about one year earlier, on 20 February 1962, had testes of exactly the same size and the bird was moderately fat. The wings of these birds measure 145.5 and 144.0 and the tails 70.9 and 70.4, respectively, which could apply to either *subis* or *hesperia*, but probably not to *arboricola* (Behle 1968). However, the fact that these birds already showed some gonadal enlargement and that *P. s. subis* arrives on the Gulf Coast of the United States as early as late January indicates that the specimens are probably referable to that subspecies. *P. s. hesperia* has

been recorded once as a fall migrant in eastern Nicaragua (Richmond 1893), but this form is not known to reach its breeding range until April (Miller et al. 1957). R. C. Banks kindly examined the pair in the U.S. National Museum, taken by Richmond on 13 September 1892, and identified as *hesperia*. Banks' measurements are: ad. ♂, wing 141, tail estimated as 67.5 (some rectrices missing); im. ♀, wing 146, tail 64.5. The female has the ventral coloration characteristic of *hesperia* and *arboricola*. The wing is too long for a female of *hesperia* and the bird might be placed with *arboricola* except that the tail is too short for that form (Behle 1968)! The male could conceivably represent any of the three subspecies recognized by Behle. Dr. Banks' opinion is that the female is probably referable to *hesperia* and presumably the associated male also, but that definite identification of either is not possible by existing criteria.

An unsexed bird in female or immature male plumage collected from a flock of 30 on 19 August weighed 49.3 and was very fat. It lacks any trace of paleness in the head region, has only slight metallic gloss dorsally, and has well-defined streaks on the abdomen. The wing measures 138.0, and the bird is probably a first-year example of *P. s. subis*.

Progne chalybea chalybea. Gray-breasted Martin. RV. The resident martins are usually found around towns and villages, especially near rivers or ponds. Although sometimes seen over the savanna, they do not forage over it to any great extent and there is no indication that they ever nest in pines. An adult male collected in Puerto Cabezas on 3 February 1955 had testes measuring 3.5 × 3, about the same size as those of the February migrants of *P. s. subis* listed above.

Stelgidopteryx ruficollis. Rough-winged Swallow. These swallows were found only along larger creeks, rivers, and ponds and did not come out over the savanna. At least two forms are present during the winter months. On 15 February 1962, a female was collected at Leimus on the Río Coco; its follicles were not enlarged. There is a distinct wash of buff on the throat, the undertail coverts are unspotted white with slightly dark shaft streaks on the longest feathers, and the wing measures 101 mm. If the buffy throat is a good character for distinguishing the middle American *fulvipennis* from the northern *serripennis*, this bird represents *fulvipennis*. However, the more southern form *uropygialis* also occurs in this region as Rough-wings seen in March 1966, along the same river, had a conspicuous light rump and could not have been *fulvipennis*. There are many specimens of *uropygialis* from Caribbean Nicaragua, and I have three birds taken in January of 1953 and 1955 at Arenal, elevation about 400 m, 25 km east of Jalapa, Nueva Segovia. This locality was then in Nicaragua but is now in Honduran territory (Monroe 1968). These specimens were overlooked by Monroe and me in compiling the Arenal records. The birds are in perfect fresh plumage and show the color characters of *uropygialis* in the highest degree; that form should thus be included in the avifauna of Honduras. I also have three January specimens of *fulvipennis*, one from Arenal and two from nearby localities at similar elevations in the Depto. de Nueva Segovia, but neither these nor the *uropygialis* had enlarged gonads. Slud (1964) reports the relationship of the more northern *serripennis* group (including *fulvipennis*) and the more southern *ruficollis* group (including *uropygialis*) needs review and clarification.

Riparia riparia riparia. Bank Swallow. M. The only one recorded is an immature male taken on 26 August at Leicus Creek as it perched with 15 Barn Swallows (*Hirundo rustica erythrogaster*). It had a single-layered skull, testes size less than 1 mm, no fat, and a weight of 11.2. There are no published records of the Bank Swallow from Nicaragua, but in the American Museum of Natural History, there is a female taken at Tipitapa, Managua, on 28 April 1917. Notes of W. deW. Miller state that a flock of about 100 was seen at that time. The species is undoubtedly far more common as a transient than these two records indicate.

Tachycineta bicolor. Tree Swallow. WR. Tree swallows are not regular winter residents, but they were present in large numbers in January and February 1963. Two specimens, both females, were collected on 23 January and 1 February; they weighed 18.3 and 17.8, and there was no enlargement of follicles. Monroe (1968) also recorded an abundance of tree swallows on the Caribbean slope of Honduras in the winter of 1962–63. We did not find the species in the savanna region or elsewhere in Nicaragua at any other time, and it seems to be of irregular occurrence south of Honduras. There is only one published record for Costa Rica and two for Panama (Wetmore 1958; Slud 1964). Although Nicaragua is included in the winter range in several recent references, I know of no Nicaraguan records other than those cited here for the first time.

Cyanocorax morio cyanogenys. Brown Jay. RV. Flocks of Brown Jays are frequent visitors to the pine savanna from the broad-leafed forest edge. They do not appear to obtain much if any food from the pine trees but sometimes feed on berries of the larger shrubs such as *Byrsonima* and *Miconia*. Two males were collected at the same locality at the savanna edge on 23 January 1962. One has a one-quarter black-tipped yellow bill, fresh unworn plumage with truncate outermost rectrices, and had testes measuring 10 × 6. The other has an all-yellow bill, very worn, tapered remiges and rectrices—the body plumage is relatively unworn—and had testes measuring only 2.5 × 1.5. These two clearly represent adult and first-year birds, respectively, as categorized by Selander (1959). A jay was seen gathering twigs on 7 February 1962 but no nests were found. Superficially, the savanna habitat appears suitable for the Green Jay (*Cyanocorax yncas*), but that species reaches the southern limit of its Central American range in western Honduras. Perhaps the visiting Brown Jay has inhibited colonization of the pine savanna by any other corvid, perhaps no others have reached this isolated habitat, or perhaps its resources are unsuitable or insufficient to support a truly resident species. For example, the dense and rather high cover of grasses and sedges over most of the savanna would inhibit the kind of ground foraging which is important to the Steller Jay (*Cyanocitta stelleri*) of the montane pine forests.

I agree with Hardy (1969) that *Psilorhinus* should be a subgenus of *Cyanocorax*.

Cistothorus platensis. Short-billed Marsh Wren. PR? This species seems to be very locally distrbuted in Nicaragua. A male obtained in a marshy area in the pine savanna about 25 miles NW of Puerto Cabezas on 12 February 1962 was the only one found although the

same place was revisited many times in subsequent years. The testes were enlarged to 4.5 × 3 mm, and there is presumably a resident breeding population in the Nicaraguan savanna as in the Honduran Mosquitia and in British Honduras. The only other record for Nicaragua is a male, "t.v.s.e.," taken 9 miles SE of San Rafael del Norte, Jinotega, on 5 April 1917; the specimen is in the American Museum of Natural History. The savanna bird is in worn plumage and cannot be definitely identified subspecifically but presumably represents *elegans*.

Sialia sialis caribaea. Eastern Bluebird. PR. A series of eight males and eight females collected since 1963 averages slightly less in wing and tail measurements of both sexes than the type series and confirms the small size dimensions of *caribaea* (Howell 1965). Most of the *caribaea* females appear slightly paler on the throat and breast than most *meridionalis* and there is a tendency in *caribaea* females for the tawny color not to extend as far posteriorly as in the latter subspecies, but these slight differences are not distinctive.

Some birds were in pairs during each month of our visits, but pairs often merged with one or two other pairs to form small groups and to join mixed species flocks in the winter months. By March, the pairs tend to remain separate and males show submaximal to full testicular enlargement, although females still show no follicular growth. In April, both sexes appeared to be in breeding condition—one female had follicles 4 mm in diameter—but no nests were found. In August, the bluebirds were in family groups of two adults and one or two immatures; a spot-breasted juvenile was seen begging unsuccessfully to its parents on 20 August. Males did not sing often, but some were heard singing in December, March, April, and August.

A male taken on 22 August was in full molt, and a female collected on 18 April showed considerable wear. Weights were as follows: 12 ♂, 26.0–34.1 (29.6); 11 ♀, 28.5–32.7 (30.2). Stomach contents included insect remains and berries.

Parula americana. Northern Parula. The only record for this species is an immature male taken in oaks at the edge of the savanna at Leicus Creek on 1 December 1968. The weight was 6.8 and the skull was single-layered. The Northern Parula is probably not associated with the pine savanna proper, but the record is cited here for its distributional interest. All standard references include Nicaragua within the winter range of the species, but the only previous record is a single bird taken by Richmond on the Río Escondido on 26 October 1892. I have never encountered this warbler elsewhere in Nicaragua, and the longtime resident collector W. B. Richardson never obtained a specimen. There is but one specimen record from Costa Rica and Slud (1964) never found it there. For El Salvador there is likewise only a single record, and Monroe (1968) states that there are no records from the mainland of Honduras although the species has frequently been taken on the islands off the north coast.

The four specimens listed above, each apparently a lone individual, are the only ones known from mainland Central America south of Guatemala and British Honduras. With only four records over at least 76 years, it is clear that the species is casual to accidental on the isthmus south of about 15° to 16° N latitude. Curiously, the Northern Parula is apparently not rare as a spring migrant on the Bay Islands of Honduras (Monroe 1968) and the keys of British Honduras (Russell 1964). These birds can scarcely be coming from farther south in Central America, and they are probably migrants from the main wintering area in the West Indies that have been carried westward toward the Central American coast by the prevailing northeast winds. It is of interest that four Northern Parulas were noted in December 1966 on Isla San Andrés (Paulson et al. 1969), 120 miles east of the Nicaraguan coast, an island with an indigenous avifauna primarily of West Indian affinities.

Dendroica coronata. Myrtle Warbler. WR. A female collected on 20 January 1963 has a wing length of 66.8, indicating as expected that it does not represent the most northwestern part of the breeding population (Hubbard 1970). Myrtle Warblers are moderately common in the savanna in the winter months, at least from November to mid-March, but were not recorded in August or April. They are locally distributed and usually found in flocks, often with some of the resident species. None of the latter uses consistently the Myrtle Warbler's foraging combination of sallying after flying insects and going to the ground within the pines.

Dendroica dominica albilora. Yellow-throated Warbler. WR. These warblers are usually found entirely alone or as a single bird associated with other species. They are moderately common in the pines at least from 21 August to mid-March; none was seen in April. Although the species occurs in broad-leafed vegetation on the Pacific slope of Nicaragua, I seldom saw them out of the pines in the northeastern sector. A Yellow-throated Warbler is so often found in close proximity to Grace Warblers, even in the same tree, that mere coincidence is unlikely. I saw a Yellow-throated Warbler supplant a Grace Warbler only once, but often noted Grace Warblers attacking or chasing the former. I have discussed elsewhere (Howell 1971) the ecological relationship between these similar-appearing species. In brief, *D. dominica* often uses its relatively long bill to probe into deep bark crevices on the trunks and larger branches of pines, often foraging in a manner similar to *Mniotilta varia* (which I have only seen once in the pines); it thus exploits resources not available to the smaller-billed *D. graciae*, which usually forages along the smaller branches and in clusters of needles.

On 11 March, I saw two Yellow-throated Warblers foraging in the same tree and they finally flew away together. This was the only instance noted of possible pair formation, and we never heard any song from this species. Females were collected on 24 August and on 20 November; both had single-layered skulls and weighed 8.7 and 9.4, respectively. An unsexed bird taken on 28 January 1962 had a double-layered skull. The latter two specimens have traces of yellow in the lores but are within the limits of variation of *albilora*.

Dendroica graciae decora. Grace Warbler. PR. This species is the most regularly distributed of all the pine savanna birds. It never ventures into trees other than pines although it may sometimes descend to patches of open ground. Grace Warblers are often the only birds encountered as one traverses long stretches of the savanna, and they are more likely than any others to be found farthest from the broad-leafed forest edge. They are in pairs throughout the year, and males were in song during every month of our visits. A singing male collected on 24 January 1962

had testes less than 1 mm in diameter, and it is likely that in this population song is independent of gonadal development. Grace Warblers singly or as a pair may appear in mixed species flocks, but the only instance in which I saw more than two of the warblers together was on 13 August when a group of three—probably a family—was noted. Some enlargement of testes begins as early as the first week of February and diameters up to 7 mm are reached by mid-March, but females show little or no follicular enlargement by that date. Nesting probably does not take place until at least the end of April, for we found no nests and saw no carrying of nest material by that time. For a discussion of foraging behavior in this species, see Howell (1971).

I assembled a series of ten males, six females, and two unsexed Grace Warblers from the pine savanna and compared these with a large series of *decora* from British Honduras. I have examined four topotypes of *remota*, two adults and two juvenals, from Volcán Viejo (= Volcán San Cristóbal), Chinandega, Nicaragua, all of which are rather worn birds taken in May. There is another topotype (female) in the Royal Ontario Museum taken by W. B. Richardson on 28 April 1891, and I obtained a male at the type locality on 28 November 1961. All of these I have compared with large series from the montane pine forests of El Salvador, Honduras, and north central Nicaragua. At the time of Webster's revision (1961) of this species, I had only one specimen from the Nicaraguan pine savanna; he assigned it tentatively to *remota*, saying that it had the color of *decora* but the size of *remota*. That specimen happens to have the largest wing and tail measurements (60.0, 48.5) of any from the savanna and is thus atypical in size. Monroe (1968) has since pointed out that the Honduras-Nicaragua pine savanna birds represent *decora*, as expected in view of the close affinities of the British Honduras and Mosquitia avifaunas. The 28 November specimen of *remota* mentioned above is the only fresh-plumaged topotype in existence, and in color it matches closely a near-topotype of *ornata* Brodkorb from Chiapas and thus supports the synonymizing of that subspecies with *remota*. Although I recognize *remota* and *decora* as distinct, they seem to me to be only slightly differentiated. The somewhat deeper yellow of the throat and more purely gray, less brown-tinged dorsum of *decora* are detectable as are the slightly smaller wing and tail lengths although the differences are not statistically significant. In the Nicaraguan savanna series of *decora*, I do not find that the bill averages any shorter or more robust than in a series of nine males and four females of *remota* from montane Nicaragua and El Salvador. My measurements of the tail in males of *decora* from the savanna average longer [44.4–48.3 (46.9)] than those of Webster (1961) of a series from British Honduras [41–48 (44.29)]. However, my tail measurements of *remota* are similarly longer than his, suggesting that the differences are artifacts of measuring technique.

Dendroica discolor. *Prairie Warbler. On 4 January 1963, I saw a single bird at close range in the pines 4 miles NW of Puerto Cabezas. This species seldom occurs in Central America and is doubtless only a vagrant in the savanna region although this habitat is superficially similar to that in which it breeds in the Gulf Coast states and might provide suitable wintering quarters.

Dendroica palmarum palmarum. Palm Warbler. WR. We found these warblers moderately common but very locally distributed in January 1962 and in that same month in 1963; they were usually in small flocks with other species such as bluebirds, Myrtle Warblers, meadowlarks, and Chipping Sparrows. On 1 December, I saw two Palm Warblers with a group that included a pair of bluebirds, a Yellow-throated Warbler, and two Grace Warblers. None was seen in August, March, or April. Single specimens were collected on 23 January 1962 and on 22 January 1963, both females; a male was collected on 31 January 1963 but the specimen was later lost.

Geothlypis poliocephala. Gray-crowned Yellowthroat. RV. These warblers are found at the edges of thickets along streams and around ponds, and they may be found in the savanna where there is herbaceous vegetation around wet areas. They were in pairs and males were in song by February. Three specimens provide the following data: ♀, 22 January 1963, wt. 13.2, no follicular enlargement; ♂, 16 March 1966, wt. 16.2, testes 6 × 3.5; ♂, 17 April 1967, wt. 16.4, testes 8 × 5.

I am unable to identify these specimens to subspecies with any confidence as they do not seem to represent either *palpebralis* or *caninucha*. I cannot attempt here to revise the entire species but will point out what I feel are unresolved problems. First, I am doubtful about the usefulness of the extent of gray on the crown and the hindneck or the greenish or brownish tone of the dorsum. The latter color especially varies so much with degree of wear that comparison of birds other than those in fresh, unworn plumage is likely to mislead. There is so much overlap in wing, tail, and culmen lengths in the populations from southern México to northern Costa Rica that these measurements are of no taxonomic value. I have paid most attention to the presence and extent of white or yellowish on the eyelids, on flank color, and especially the depth and extent of yellow on the underparts.

Ridgway (1902) characterized *palpebralis* as having "the under parts entirely yellow" and with extensive white or yellowish on the upper and lower eyelids; the type locality is Mirador, Veracruz. I have examined 20 males and seven females in the Moore Collection from the state of Veracruz, all collected by C. C. Lamb; unfortunately, most are in worn plumage. All have extensively pale eyelids, and although all have "entirely" yellow underparts, this color is distinctly paler on the abdomen. Two males and four females from Oaxaca and one male from 3 miles SSW of Tonalá, Chiapas, are like those from Veracruz.

Somewhere in Guatemala, apparently, the extensive light color of the eyelids is reduced or disappears. South of Guatemala some birds show varying amounts of light color, usually a tiny spot on the posterior half of the upper eyelid, but I have seen none that resemble typical *palpebralis*. Ridgway (1872) described *caninucha* from a single specimen from Retalhuleu in the Pacific lowlands of Guatemala. By 1902, he still had only one specimen, the type, from that country but assigned all birds from Honduras, Nicaragua, Costa Rica, and Panamá to *caninucha*. At that time, Ridgway believed *caninucha* to be specifically distinct in lacking pale eyelids, and he gave no detailed comparisons between that form and *palpebralis*. Ridgway's treatment seems to have created two impressions in particular: (1) that

caninucha is more completely yellow on the underparts than any other population; (2) that *palpebralis* is distinguishable from more southern populations only on the basis of pale eyelid markings. Possibly noticing that this character becomes variable south of México, Miller et al. (1957) considered *palpebralis* a synonym of *caninucha*. Wetmore (1944) reviewed all the subspecies; he gave the range of *palpebralis* as central Veracruz through northern Chiapas to eastern Guatemala, and that of *caninucha* as southern Chiapas through western Guatemala, Honduras, and eastern Nicaragua. Wetmore characterized *caninucha* as "similar to *palpebralis* but brighter green above; yellow on lower surface more extensive, covering the abdomen." He recognized another form, *icterotis*, from western Nicaragua to central Costa Rica. The range given for *caninucha*, if correct, is most unusual. One would expect a consistent division between Pacific slope and Caribbean slope populations instead of having the same subspecies (*caninucha*) extending broadly across both slopes, with a different eastern slope form (*palpebralis*) to the north and a different Pacific slope form (*icterotis*) to the south.

I have not seen specimens from Guatemala but have examined six males and one female from El Salvador; these should represent *caninucha* as El Salvador is continuous with the Pacific slope of Guatemala from whence the type came. Contrary to the characterizations given above, I find these birds not to be uniformly yellow on the entire underparts but to have the abdomen paler yellow than the rest and to have pale brownish flanks. This is also the case with birds from the Pacific lowlands of Honduras. On the other hand, birds from Caribbean Honduras and Caribbean Nicaragua, including the pine savanna, are uniformly and more deeply yellow on the underparts and darker brown on the flanks. Those from western Nicaragua are paler and less extensively yellow ventrally. None of these specimens has more than traces of pale spotting on the eyelids.

I have not examined a definitive series, but suggest the following rearrangement as a working hypothesis:

1) *palpebralis*: extensive pale eyelid spots; underparts yellow, distinctly paler on the abdomen; northern Veracruz through northern Chiapas to British Honduras and eastern Guatemala.

2) *caninucha*: pale eyelid spots much reduced or absent; underparts yellow, slightly paler on abdomen; extreme eastern Oaxaca and southern Chiapas, Pacific slopes of Guatemala, El Salvador, and Honduras, extending into northwestern Nicaragua.

3) subspecies?: pale eyelid spots reduced or absent; yellow of underparts deeper and more uniform, not paler on abdomen or only faintly so; flanks darker brown than in *caninucha*; from eastern Guatemala (where intergrading with *palpebralis*?) south over most of Honduras except the southwest portion and over the entire Caribbean slope of Nicaragua, probably into northeastern Costa Rica.

These ranges are essentially the same as those given by Lowery and Monroe (1968) except that I have separated the southern portion of their range for *palpebralis*. This population may be an undescribed form but should not be named until an extensive sample of all the populations between México and Panamá is assembled and compared. The distinctions between *caninucha* and *icterotis* should also be reviewed, and the former recharacterized from topotypical or near-topotypical material only.

Icterus chrysater chrysater. Yellow-backed Oriole. PR. These orioles are sparsely distributed throughout the pine savanna, sometimes venturing into oaks or other broad-leafed trees. They seem to go in pairs throughout the year but may assemble in flocks of at least six birds during the winter months and may also join mixed species flocks. Singing was heard in all months of our visits except August. On 28 January 1962, a pair was collected, both members of which were heard singing. The male had testes measuring 3×2 and the follicles of the female were unenlarged. Skutch (1954) mentions singing by females in *I. mesomelas*.

The Yellow-backed Oriole forages in the pines and also in the epiphytes such as mistletoe and bromeliads. On 20 April, I saw first one and then the other member of a pair fly about 50 m directly to a bromeliad in a pine and several times dip their bills in among the leaves, presumably drinking but possibly obtaining insects. On 29 November, I saw a male foraging a large pine by poking its bill into bark crevices along the larger branches; a female collected on 17 April has a lump of rosin along the culmen and may also have been probing in bark crevices. Weights recorded are: ♂, 58.9, 61.5; ♀, 51.8, 52.3. A series of four males and five females was collected, and despite the isolation of the pine savanna population, I can detect no difference in color or size from birds from montane Nicaragua and El Salvador. A singing male taken on 28 January 1963 is unusually highly colored, with a distinct wash of orange tinging the back, sides of neck, and the mid-ventral region of the breast and abdomen.

Agelaius phoeniceus. Red-winged Blackbird. The Royal Ontario Museum has an adult male (ROM 6457) collected at "Klupki on Rio Wanks 20 miles above Cape Gracias" by M. G. Palmer on 21 January 1904. This bird's measurements are: wing, 106.1; tail, 78.4; culmen from nostril, 15.8; these place it in the size range of *brevirostris* (Monroe 1963). I have not found this species in the savanna region even in marshy areas that appear suitable for it.

Sturnella magna inexpectata. Eastern Meadowlark. PR. Meadowlarks occur throughout the savanna except within dense stands of trees or in completely treeless grassland. They were in small flocks of up to eight birds in August and November, with some indication of pairing in the latter month and with both pairs and flocks in late January. From February into April pairs are the rule, but song was heard in all months of our visits. In March and April, we heard a form of duetting in which the male sang the typical whistled song and the female added a rattling or chattering call either before the male's song was completed or just after. In late January and early February, males had testes sizes ranging from unenlarged up to 4×3; females showed no gonadal enlargement. From mid-March to late April all males had much enlarged testes up to 14×6, but of four females, two showed no follicle enlargement and two had slightly enlarged follicles 1.5 to 2 mm in diameter. None had an incubation patch, and no nests were found.

Dickerman and Phillips (1970) examined my series of meadowlarks and pointed out the remarkably small size that characterizes *inexpectata*, which is by far the smallest of the *S. magna* subspecies. I agree with their characterization of this form and the restriction of its range to the pine savanna of Nicaragua and Honduras, and also agree with Eisenmann's (1970)

reasons for retaining the spelling *inexpectata* instead of the original *inexspectata*.

Piranga flava savannarum. Hepatic Tanager. PR. The measurements of six males and one female collected subsequent to the type series (Howell 1965) all fall within the previous ranges and do not alter the means by more than 0.1 mm. Except for the Grace Warbler, this is the most regularly distributed of the arboreal species and may be found in pines far from broad-leafed vegetation although the tanagers may utilize nonpine trees at the edge of the savanna to some extent. Hepatic Tanagers were paired in all months of our visits and a pair often joined a mixed species flock. Most of their food seems to be obtained from pines, but they were also seen feeding on berries of the shrub *Miconia lundelli* and may occasionally descend to the ground, possibly after insects. One stomach contained remains of large ants.

Plumages of males are sometimes puzzling. A male taken on 22 August had a double-layered skull and unenlarged testes; it was in molt from worn green to fresh red plumage. Another male taken on 26 August had a single-layered skull and unenlarged testes and thus must have been a bird of the year; it is similar in color and in state of molt. However, a male in fully green plumage collected on 11 March had a double-layered skull and testes enlarged to 6×4. The plumage is not much abraded except for the three innermost primaries on either side. Other males in fully red plumage taken in March and April had testes sizes ranging from 8×4 to 10×7. A female taken on 17 April had a slightly enlarged follicle measuring 1.5, and was in very worn plumage but had no trace of an incubation patch. On 18 April, I saw the male of a pair of Hepatic Tanagers gathering nest material and carrying it in his beak, and on 28 April, I saw actual nest construction by a female with a nest site about 10 m up in a small pine that was about 12 m high. The female gathered fibers from epiphytes in pines, then flew to the site in a cluster of pine needles. The male of this pair was close by and appeared to follow the female but did not gather any material or go to the exact site.

Remarkably, we never heard any song whatsoever from these tanagers. Males on conspicuous high perches gave only single notes from time to time, even in March and April. Possibly the absence of song is associated with conspicuous sexual dimorphism in color of definitive adults and the absence of any similar-appearing species in the pines.

Monroe (1968) records specimens referable to *albifacies* in color but of small size approaching that of *savannarum* from San Estéban, Olancho, a locality about 50 miles west of the margin of the savanna in eastern Honduras. I suspect that some gene flow between the montane and savanna populations occurs in this region, as may also be true of *Sialia sialis* (Howell 1965).

Guiraca caerulea caerulea. Blue Grosbeak. WR? We saw flocks of these grosbeaks, mostly males, in February 1962 and again in March 1966, usually in stands of cane grass (*Tripsacum* sp.) at the interface of the savanna and broad-leafed thickets. We saw none in any of the other months. The birds were usually very wary and we obtained only two specimens, a female on 12 March and a male on 14 March. Relevant data are: ♂, wing 87.6, tail 67.5, culmen from nostril 12.1, wt. 30.0, slightly fat, testes 2×1; ♀, wing 83.4, tail 65.5, culmen from nostril 11.6, wt. 29.5, slightly fat, follicles smaller than 1 mm.

In size and color, both birds are referable to *G. c. caerulea* and not to *lazula*, the subspecies that breeds on the Pacific slope of Nicaragua. There are no other records of *G. c. caerulea* from Nicaragua, but it seems likely that all those seen belonged to that subspecies. Whether the birds seen and collected were winter residents or early spring migrants on their way north is impossible to determine. The preponderance of males in the flocks was quite striking as they outnumbered females, when present, by about 6:1.

Sicalis luteola chrysops. Grassland Yellow-Finch PR? These finches seem to be erratic wanderers in flocks, and I found them in only one locality—the extensively marshy area about 25 miles NW of Puerto Cabezas that also provided the only records for the Plain-breasted Ground-Dove and the Short-billed Marsh Wren. I saw a flock of about 50 on 13 February 1962 among tall herbaceous plants in the marsh. The finches were very noisy and nervous, and after one unsuccessful shot, the entire flock rose and flew out of sight across the savanna. They were not seen again in 1962, but on 1 February 1963 a flock of from 35 to 50 birds was again present at exactly the same place, swirling around in a tight group and uttering continuous buzzing and twittering calls. Some alighted in the grass and others in a *Curatella americana* tree at the edge of the marsh, and they stayed so close together that a single shot got five birds. Two of three males weighed 13.3 and 14.0 and had testes slightly enlarged to 2×2 and 4×3 mm; one of two females weighed 12.5, and neither showed any enlargement of follicles.

I agree with Monroe (1968) that the pine savanna finches represent *chrysops*. I know of no previous published record from Nicaragua, but on 1 August 1953 I saw a flock of this species in the tall grass at the edge of the airfield at Bluefields, Zelaya, Nicaragua. I never encountered these birds in grasslands on the Pacific slope of Nicaragua nor did van Rossem find them in El Salvador. Slud's (1964) sight records from the arid northwest quadrat of Costa Rica may pertain to *S. l. eisenmanni* of western Panamá.

Ammodramus savannarum cracens. Grasshopper Sparrow. PR. In the pine savanna we found this sparrow only at the edges of low wet places in the grasslands, and it was not common there in contrast to its status in Honduras (Monroe 1968). A male collected on 30 January 1963 weighed 14.7 and had testes measuring less than 1 mm. In March, males were in song and the birds were paired. Data from birds collected in 1966 are: a pair, 14 March, ♂, wt. 15.6, testes 8×5 and 2×2; ♀, wt. 14.4, follicles $<$ 1 mm; and 24 March, ♂, wt. 15.7, testis 9×6. The small series appears typical of *cracens* in size and color.

Aimophila rufescens discolor. Rusty Sparrow. PR. This is the most common of the nonarboreal savanna species, inhabiting grasses and sedges in areas with rocks, shrubs, or trees for song and lookout perches—usually within easy flight of a wet place or streamside thicket. The birds were in song during each month of our visits, and they sang from any exposed perch from just above grass-sedge level to the top of a 30-m pine. In August, we often saw small family groups of two adults and one or two streaked juveniles, and a streaked juvenile with an adult on 7 February 1962 indicates that there are occasional unseasonal nestings. Otherwise, these sparrows were seen singly or in pairs and never in flocks, with the singing males

much more conspicuous than the females. By February, testes may be slightly to considerably enlarged (7 × 4), but only one out of six females taken in late January to early February had enlarged follicles (2.0 mm). A female collected on 17 April had follicles enlarged to only 1.5 mm and lacked an incubation patch.

Ridgway's "description" (1888) of *discolor* from the Segovia River was only a guess as to what differences might exist in a less abraded series than the seven birds that he examined. I have compared birds taken in the Nicaraguan savanna in late November (2 ♂), late January and early February (7 ♂, 6 ♀), mid-March (2 ♂), and mid-April (1 ♀) with a series of *pyrgitoides* from Veracruz, México, made up of birds taken in November (1 ♂), March (4 ♀), late April and early May (4 ♂, 1 ♀), and August (2 ♂, in worn plumage). I cannot see any difference in coloration between the two series that is not attributable to individual variation or to wear, nor can I distinguish the allegedly heavier bill of *discolor*. As neither Russell (1964) nor Monroe (1968) nor I can distinguish *pyrgitoides* from México from birds from British Honduras and the Mosquitia on the basis of color, the only reason to maintain *discolor* would be smaller size. Wing measurements of birds from the Caribbean lowlands from México to Nicaragua are given below. Rectrices in this species are subject to such heavy wear that I do not consider tail measurements useful. Data are as follows: Veracruz, Tabasco, and Oaxaca, 11 ♂, wing 68.0–74.8 (71.3), 7 ♀, wing 67.8–71.3 (69.0); British Honduras, 16 ♂, wing 66–72 (70.0), 6 ♂, wt. 30.0–38.9 (34.4); 3 ♀, wing 63.0–65.5 (64.6), 2 ♂, wt. 28.2, 31.4; and Mosquitia, 11 ♂, wing 66.9–71.5 (69.0), 10 ♂, culmen from nostril 10.3–11.0 (10.7), 6 ♂, wt. 33.9–38.7 (36.3), 8 ♀, wing 62.3–66.5 (64.1), 7 ♀, culmen from nostril 10.4–11.4 (10.8), 2 ♀, wt. 32.2, 33.3.

I have not included Ridgway's measurements of Townsend's birds from the Segovia River as Ridgway (1901) stated that the birds were in much-worn plumage and he did not even give measurements for the two females. However, his mean of 70.6 for four males is slightly higher than that for my relatively unworn series, and Monroe informs me that he did not consider wear of the primaries excessive in the Segovia River birds. The two females collected by Townsend measure 63.0 and 65.9, and one collected by Monroe in April 1964 measures 64.2; the mean is thus 64.4, very close to my figure, and the mean of 63.7 given by Monroe (1968) is a *lapsus*. Bangs and Peck's (1908) measurements, which they gave to the nearest millimeter, are included, as are weights cited by Russell (1964) and those I obtained.

Wing length clearly varies clinally from north to south in males and would provide no grounds for subspecific division. This fact undoubtedly led Russell (1964), who did not consider size of females, to assign British Honduras birds to *pyrgitoides*. However, females from British Honduras and the Mosquitia have much shorter wings than those from México; in the present sample there is no overlap. The British Honduras-Mosquitia birds also show much greater sexual dimorphism in this character, with virtually no overlap in wing length between the sexes. Males in these populations average heavier than females, but bill length is essentially the same. In view of these differences between *pyrgitoides* from México and the British Honduras-Mosquitia birds, I tentatively retain *discolor* as the subspecies for the latter populations. The sample of females is unfortunately small, and more specimens in fresh plumage are needed to determine the true status of *discolor*, but it seems certain that the Rusty Sparrows of British Honduras and the Mosquitia belong to the same subspecies.

Aimophila botterii spadiconigrescens. Botteri Sparrow. PR. Three males of this secretive species were obtained subsequent to the collection of the type series (Howell 1965); relevant data are as follows: ♂, 12 March 1966, testes 2 × 2; wt. 19.5; ♂, 18 April 1967, testes 7 mm in diameter; wt. 18.8; skull single-layered in mid-dorsal area, otherwise double-layered; ♂, 20 April 1967, testes 6 × 4; wt. 20.3; cloacal protuberance present; lower mandible plumbeous gray, upper blackish with buffy tomium.

These birds do not differ appreciably from the fresher-plumaged type series in the chestnut-and-blackish tone of the dorsum, as described by the subspecific name. The two April-taken birds show fading from brownish to grayish on the wing coverts, and in one of these specimens the pectoral band is paler and grayer than others in the series. Dickerman and Phillips (1967) present evidence of intergradation of populations sometimes segregated specifically as *botterii* and *petenica*, and their treatment of the entire complex as conspecific is followed here.

Botteri Sparrows are doubtless not as scarce in the savanna as the few specimens suggest. They seem to be confined to grassy areas within about 50 m of palmetto-bordered wet places. When flushed, the sparrows head for the palmetto clumps and take refuge there. Males sing from low stumps or pine seedlings, generally less than 1 m above ground. On 5 February 1962, I diagrammed the song as — ‾ — — ~~~~~~; four whistled notes followed by a trill. We did not hear any songs in August or November but could easily have missed them. Some males appeared to be in breeding condition as early as the first week of February, and the breeding season extends at least to late April.

Spizella passerina pinetorum. Chipping Sparrow. PR. This is an irregularly distributed species that is common in some localities within the pine savanna and absent from others. Chipping Sparrows feed extensively on seeds of the broom-sedge grass, *Andropogon* sp., but the grass may be abundant in some locations where the sparrows are absent. Flocks of at least 25 individuals were seen in August and in January, and they may join other species such as siskins, bluebirds, and warblers in mixed flocks as late in the spring as mid-March. Single birds or pairs may be found in February and March, and in mid-April all were in pairs and strongly territorial. Songs were heard only in March and April, and the song is a dry, slow trill like that of more northern populations. I estimated four territorial males in about 5 acres where the species seemed to concentrate. The patchy distribution of groups of breeding pairs and the approximate territorial size of 1 to 1.5 acres appear to prevail in much of the species range in both temperate (Walkinshaw 1944) and tropical latitudes (Dickey and van Rossem 1938). On 20 April, I flushed a singing bird from a small pine and it flew about 30 m to another tree. Another Chipping Sparrow immediately flew to the attack, chased and caught the first bird, and they struggled and fought in mid-air, fluttering almost to the ground before separating. Two males collected on 18 and 20 April had entirely black bills, testes 8 to 9 mm in diameter, and in the

TABLE 4. Measurements of *Spizella passerina* from southern México and Central America.

Locality	Sex	n	Wing ($\bar{x}$)	n	Tail ($\bar{x}$)
Oaxaca, Chiapas	♂	7	70.2–72.4 (71.0)	5	58.3–62.6 (59.8)
	♀	3	65.7–69.5 (67.8)	4	55.4–61.0 (58.5)
Montane Central America	♂	15	67.8–73.0 (70.1)	16	55.5–60.4 (58.2)
	♀	11	64.5–69.7 (67.1)	11	53.4–59.5 (55.7)
British Honduras,	♂	4	65.9–67.2 (66.5)	4	52.2–56.0 (54.2)
Petén	♀	2	63.6–67.6 (65.6)	2	51.4–52.7 (52.1)
Nicaraguan savanna	♂	9	64.2–68.6 (66.1)	9	54.2–57.0 (55.0)
	♀	10	61.0–66.3 (63.3)	7	50.6–56.3 (53.0)

			$\bar{x}$	S.D.	S.E.	C.D.		$\bar{x}$	S.D.	S.E.	C.D.
Montane areas combined	♂	22	70.4	1.46	0.315		21	58.6	2.03	0.444	
	♀	14	67.3	1.70	0.472		15	56.5	2.30	0.594	
Caribbean areas combined	♂	13	66.2	1.19	0.331	1.57	13	54.8	1.41	0.393	1.11
	♀	12	63.7	1.82	0.526	1.02	9	53.2	1.65	0.55	.84

latter bird a cloacal protuberance. Three males taken on 12, 13, and 21 March had testes sizes 4 × 2, 7 × 5, and 7 × 4, respectively, and entirely black bills except for the last male which has traces of horn color at the base of the lower mandible. Two females taken on 13 and 21 March did not have enlarged follicles and lacked black bills. One male taken on 5 February 1962 had testes slightly enlarged to 2 × 1.5 mm, but another taken on the same day and nine others taken in late January had unenlarged gonads.

I have compared my series of 19 birds from the Nicaraguan savanna with the type of *S. p. cicada* and seven topotypes from El Salvador, 20 from north-central Nicaragua and Honduras, nine from British Honduras and Petén, Guatemala, and 12 from Oaxaca and Chiapas, México. I conclude that there is a small-sized subspecies with a range from British Honduras and Petén to the lowland pine savannas of eastern Honduras and northeastern Nicaragua. A larger form is found at least from Oaxaca south through the montane regions of Guatemala, El Salvador, Honduras, and Nicaragua. There is no diagnostic color difference between these populations, and the subspecies *cicada* Dickey and van Rossem becomes a synonym of *mexicana* Nelson (type locality San Cristóbal, Chiapas) as it agrees in size with that form, not with the lowland population. Measurements of specimens in good plumage condition are given in table 4.

There are no statistically significant differences between the mean measurements of birds from the Nicaraguan savanna and from British Honduras and Petén, nor between those from montane Nicaragua, Honduras, and El Salvador and those from Chiapas and Oaxaca. When the Caribbean pinelands birds are lumped together and compared with the combined highland pine birds (table 3, bottom), the differences between the means of comparable measurements in the two groups are all statistically significant, and in the wings of males the coefficient of difference is well above the figure of 1.28 usually used as an index of recognizable subspecific distinction.

Although the two populations appear to be distinguishable, there remains a nomenclatural problem. The form *pinetorum* was described by Salvin from a single bird collected at Poctum, Petén, Guatemala; this locality is only about 40 miles from ecologically similar areas in British Honduras and the type specimen should represent the Caribbean pinelands population and thus provide an available name. However, the only published measurements are those of Ridgway (1901)—wing, 71.12; tail, 62.23 (*sic*)—and these are considerably larger than those of any other Caribbean slope individual of *S. passerina* and exceed the means for these dimensions of the montane population. These large dimensions probably led Hellmayr (1938) to assign birds from montane Nicaragua to *pinetorum* and to suggest that *cicada* was a synonym of *pinetorum* rather than of *mexicana*. The type should be re-examined but this is unfortunately impossible at present because of the move of British Museum specimens from London to Tring.

Carduelis notata oleacea. Black-headed Siskin. PR. Siskins are moderately common but irregularly distributed throughout the pine savanna and are strictly confined to that habitat. They may form small flocks of up to 10 birds at any time of year or join mixed flocks but they may also be found as single birds or pairs at any time, and pairs may be maintained within a flock. This behavior may be related to their food supply, for they seem to depend primarily on the seeds of the abundant sedge *Hypolytrum schraderianum*. At any season some plants of this species have seed-bearing heads, and individuals, pairs, or flocks of siskins may wander widely to obtain this food. On 19 April, I saw a siskin probing into bark crevices on the small branches of a pine; it then abandoned this unusual activity and joined its mate in feeding on *Hypolytrum* seeds.

Males were in song in each month of our visits except August. Of 10 adult-plumaged males collected from late November to mid-April, all had testes enlarged to 5 or 6 mm in diameter except a 25 November bird (1.8 mm) and a 1 December bird (1 mm). However, another male taken from the same flock on 1 December had testes measuring 6 × 4. Females taken on 30 November, 1 December, 31 January, and 16 March showed no follicular enlargement, but another taken on 31 January had an ovary that appeared to be post-laying although there was no incubation patch. One taken on 17 April had a well-developed incubation patch and follicles enlarged to 2 mm. The female taken on 30 November was in heavy molt, with remiges and rectrices under replacement and black feathers replacing greenish ones on the head. The female taken on 16 March

TABLE 5. Measurements for *Loxia curvirostra mesamericana.*

Locality	Sex	n	Wing	n	Tail	n	Culmen from nostril
Montane Honduras	♂	13	86.7–94.3 (90.2)	14	48.8–55.5 (52.1)	15	15.3–17.0 (16.2)
and Nicaragua	♀	9	82.0–90.9 (87.0)	10	46.3–52.2 (50.6)	11	14.8–16.7 (15.7)
British Honduras	♂	6	85.3–88.7 (87.2)	5	48.8–51.5 (49.9)	6	16.7–18.5 (17.4)
and Mosquitia	♀	5	82.0–88.0 (84.8)	5	48.0–50.3 (49.1)	5	16.7–17.3 (17.1)

was still largely in worn juvenile plumage except for a mottling of black feathers on the head. In August, I saw one flock of 10 immature birds, all with green heads, and also saw a presumed family group of three immatures and one black-headed adult. On 27 November, I encountered a pair in which the male sang frequently and once seemed (partly obstructed view) to feed the female. The pair appeared to occupy an area about 150 m in diameter. On 1 December, I met a sociable flock of about 10 siskins flying down from the pines to feed on *Hypolytrum* seeds. I collected three birds from this flock, and all had crops containing up to 40 of these seeds, which are spherical and about 1.5 mm in diameter. This flock contained at least three birds with greenish mottling on the head. Of two males collected, one with much-enlarged and the other with unenlarged testes, the plumage appears identical and the skulls also—double-layered, but thin and translucent. It appears that there is a long breeding season within the savanna population, extending from at least late November through April.

Weights recorded were: five ♂, 9.8–12.5 (10.9); six ♀, 9.3–11.2 (10.4).

I compared the Nicaraguan savanna series of 10 males and six females with series of 20 males and 10 females from montane Nicaragua, El Salvador, and Honduras, and eight males and three females from British Honduras. The British Honduras birds agree in size and color with the nonsavanna birds, and all may be assigned to *oleacea.* The Nicaraguan savanna population differs slightly from typical *oleacea* in that males average lighter, brighter yellow on the underparts, especially the abdomen, and average lighter green on the back, with less subterminal black markings; the females, however, do not appear to differ in color from *oleacea.* Relevant measurements for the Nicaraguan savanna are: 10 ♂, wing 59.7–65.7 (62.4), culmen from nostril 10.3–11.0 (10.6), S.D. = 0.25, C.D. = 1.7; and 5 ♀, wing 57.6–61.1 (59.5), 6 ♀, culmen from nostril 9.8–11.3 (10.2), S.D. = 0.58, C.D. = 0.74. Those for *oleacea* are: 28 ♂, wing 61.5–65.9 (63.6), culmen from nostril 8.8–10.5 (9.5), S.D. = 0.39; and 13 ♀, wing 59.3–62.9 (61.3), 12 ♀, culmen from nostril 9.0–10.0 (9.5), S.D. = 0.37. Wing length in both sexes of the savanna birds averages slightly shorter, but the differences are not significant. The bill is longer in the Nicaraguan savanna birds, as shown by culmen-from-nostril measurements.

The coefficient of difference (C.D. = difference between means of the two samples/sum of their standard deviations) in culmen length is 1.7 for males but only 0.74 for females. The difference in males is statistically significant and "taxonomically significant" as the C.D. exceeds 1.28 and there is almost no overlap; however, there is no significant difference between the females although the culmen averages longer in the savanna birds. The savanna population thus approaches subspecific distinction from *oleacea,* but I prefer not to propose formal recognition. The most cogent difference is in culmen length, which could be influenced by degree of wear at the tip. The savanna siskins seem to feed principally upon *Hypolytrum* seeds which can be extracted with virtually no abrasion of the bill. It is conceivable that this accounts for the relatively long measurements although I have no evidence that *oleacea* populations feed in a more bill-stressing manner. In view of the slightness of the difference and the lack of statistical significance of differences in females, I refer the savanna siskins to *oleacea.*

Loxia curvirostra mesamericana. Red Crossbill. PR. I was greatly surprised to encounter crossbills in the lowland pines, and they appeared to be resident but very scarce. Despite constant watchfulness, we obtained only six specimens and saw few others. We collected three males in early February 1962 and one female in late January 1963; at those times the birds were paired. Testes sizes of males were 4 × 3, 5 × 3, and 5 × 4, and the female showed very slight follicular enlargement. Two other females taken on 22 August 1965 and 27 November 1966 did not have enlarged follicles. Weights of the three females were 32.7, 33.4, and 33.9. The August specimen was the only crossbill in a mixed flock of bluebirds, tanagers, warblers, and siskins. Nearby on the same day, I saw a flock of about 10 crossbills high in a pine, but they flew far out of sight when I approached closely. All that we saw were in pines, and one January bird had pine seeds in its crop. I cannot satisfactorily account for the scarcity of this species as it has no apparent competitors for the abundant and seemingly year-round crop of pine seeds.

I assign the savanna crossbills to *mesamericana* provisionally after comparing the six birds listed above with five from British Honduras and 28 from the highlands of Honduras and north-central Nicaragua. Despite Griscom's (1937) characterization of *mesamericana* as a very dark form, I can see no consistent difference in color between the Honduras-Nicaragua series and examples of *stricklandi* from México. Those from British Honduras have worn body plumage and are unsuitable for color comparison. Subspecific distinctions must therefore be made on the basis of size. The entire series from British Honduras-Honduras-Nicaragua divides into two groups —those with longer wings and tails and shorter bills, from the highlands, and those with shorter wings and tails but longer bills, from British Honduras and the Nicaraguan savanna. The measurements are shown in table 5.

The means for wing length and culmen-from-nostril length (chord) are significantly different between the sexes in each population, but only in culmen length in females does the C.D. reach a "significant" level (C.D. = 1.52). The bills of the Caribbean pinelands birds appear to have slightly straighter culmens and

FIGURE 2. Red Crossbills from montane Central America and the Caribbean pinelands, showing relative bill sizes. The bills of the specimens shown are within 0.2 mm of the mean culmen-from-nostril length for each sex in each population. Left to right: male, montane Honduras; male, British Honduras; female, Nicaraguan pine savanna; female, montane Honduras.

to be generally larger (fig. 2), but these birds deal entirely with the small cones of *Pinus caribaea* and their bills may be less subject to stress and wear at the tip than those of montane birds that deal with the larger cones of *Pinus oocarpa*. The crossbills of British Honduras and the Mosquitia may be distinct from *mesamericana*, but the sample size is too small as yet to justify nomenclatural recognition.

DISCUSSION

The genus *Pinus* is almost entirely confined to the Northern Hemisphere and pines are unquestionably of north temperate zone origin. *Pinus caribaea* occurs primarily in tropical latitudes at low elevations and has a peculiar disjunct distribution. It is found on some of the Bahama Islands, in Pinar del Río province in western Cuba, and on the Isle of Pines, and irregularly in Central America, primarily on the Caribbean slope, from British Honduras to central Nicaragua. Isolated patches of *P. caribaea* are found inland to eastern Guatemala, and it is widespread in the interior of Honduras at low elevations and less widespread in the lower elevations of the Nicaraguan highlands. The species is generally found below 1000 m in altitude, and in Honduras and Nicaragua there is no known continuity between the inland pine stands and the coastal population. According to Critchfield and Little (1966), *P. caribaea* belongs in the subgenus *Pinus*, section Pinus, subsection Australes, which includes 10 other species. Two of these are confined to the West Indies, and the other eight are found in eastern North America, with none occurring west of east Texas. *P. elliottii*, the Slash Pine of southeastern United States including peninsular Florida, is apparently the species most closely related to *P. caribaea*; the two have previously been considered conspecific. None of the pine species found in montane Central America is in the same subsection of the genus as *P. caribaea*. Thus, the closest affinity of *P. caribaea* is not with the nearby montane species but with those of the coastal plain of southeastern United States and the West Indies.

How *Pinus caribaea* attained its disjunct distribution is an open question. Cuba was not connected to Florida during the Cenozoic era. Asprey and Robbins (1953) accept Schuchert's (1935) proposed land bridges between Honduras and the Greater Antilles during the Tertiary but regard Cuba's two species of *Pinus*, along with six other genera of trees, as having reached the island from North America. Mirov (1967:48–51) leans to the idea that pines reached the West Indies and possibly southern Florida from Central America. Little and Dorman (1954), in the most complete review of the evidence, state that "It is not known in which direction migration may have occurred," and they point out that there is no relevant fossil record.

To account for the peculiar distribution of *Pinus caribaea-P. elliottii* complex, I can envision the following alternatives:

1) An ancestral population ranged (not necessarily simultaneously) from southeastern United States through Mexico and Central America to Nicaragua; the populations between the present ranges of *caribaea* and *elliottii* disappeared, leading to differentiation into those two species; *caribaea* then dispersed from Central America to Cuba and the Bahamas.

2) *P. caribaea* evolved in Central America and dispersed to Cuba, the Bahamas, and to southeastern United States, where the population differentiated into *P. elliottii*.

3) An ancestral population in southeastern United States spread to Cuba, where *caribaea*

differentiated; *caribaea* then dispersed relatively recently to the Bahamas and to the Caribbean coast of Central America, where it once ranged continuously from British Honduras to Nicaragua and where it has since spread inland, especially in Honduras.

Considering the first alternative, I find it difficult to explain why *caribaea-elliottii* should have disappeared totally, without even a small relict population, from the entire region between eastern Louisiana and British Honduras. There are many cases of disjunct distributions that provide evidence of former floristic and faunistic connections between eastern North America and the highlands of México and Central America (Martin and Harrell 1957), but these are marked by the presence of relict populations north of the Isthmus of Tehuantepec. According to Munro (1966), *P. caribaea* is not resistant to frost. This could account for its absence from higher elevations and nontropical regions, but not from lowlands in southeastern Mexico where frost-intolerant plants abound and where there are savannas that look suitable for pines but which lack them. Many other species of pines occur in the highlands of Mexico, and *P. caribaea* co-exists with other pine species at moderate elevations farther south. A former continuity or overland dispersal route between the present ranges seems to me unlikely.

I also find the second alternative unlikely. As previously noted, *caribaea* belongs to a subgenus and subsection that does not include any of the contemporary Mexican and Central American pines but comprises mostly species now found only in eastern North America. Contemporary *P. caribaea* is not frost-resistant, and presumably its ancestral populations, if they differentiated in the tropics, were not frost-resistant either. It is therefore extremely unlikely that this species colonized temperate eastern North America from a tropical center of origin. A Central American origin for *caribaea* would also require a connection or dispersal route for its ancestors comparable to that discussed under the first alternative, and this is equally doubtful for the same reasons.

The third alternative is to me the most probable. Pine cones may be carried for long distances over water, and pine pollen is readily dispersed by winds (Little and Dorman 1954). At present, the strongest current in the Caribbean Sea flows northwestward between Central America and the Greater Antilles, which would not favor dispersal from Cuba to Central America by drifting. However, currents may have had a different pattern during the Pleistocene, when glacial and interglacial periods caused considerable changes in sea levels and coastal contours. The prevailing winds along the Caribbean coast are from the northeast, and hurricanes that blow across the Caribbean Sea to Central America from the Antillean region are frequent. These or lesser storms could force floating pine cones for long distances across water. It is possible, at least, that aboriginal Indians carried cone-bearing pine branches with them for torches and thus may have been agents of dispersal, but this is pure speculation.

If one concedes that pine seeds could have come from Cuba to the Carribbean coast of Central America, one must also postulate the presence there of open areas where pines could grow and reproduce. Again I see three possible alternatives:

1) Hurricanes could deforest large areas that would then be subject to fires. Russell (1964) cites the case of a hurricane which struck the coast of British Honduras on 31 October 1961, and devastated several hundred square miles of forest; fires later penetrated into the damaged hardwood stands (Munro 1966). On 10 September 1971, a devastating hurricane struck the Caribbean coast of Honduras and Nicaragua and moved on to British Honduras. Then, in mid-November 1971, another hurricane swept across Pinar del Río Province, Cuba (where *P. caribaea* occurs) and proceeded with diminished force to British Honduras.

2) Early aborigines may have cleared and burned large areas of forest, with clearings maintained and extended by dry season fires. I know of no evidence that this happened before historic times, but such practices maintain the pine savanna today.

3) Cyclic periods of aridity during the Pleistocene may have greatly reduced the extent of humid forest and resulted in grassy savannas suitable for colonizing by pines. Vuilleumier (1971) provides new data and a summary of previous evidence that this took place in South America, and there must have been similar arid periods in Central America.

None of the three alternative explanations necessarily excludes the others. The arid period hypothesis suggests a greater extension back into geologic time, but aridity may have established savannas that were much later colonized by pines. The ages and former distributions of the species *elliottii* and *caribaea* are not known, but one may make inferences about the age and extent of the lowland pine savanna.

The Honduran-Nicaraguan Mosquitia corresponds closely to an area of Pleistocene sediments (Taylor 1963), and the present coastal lowlands distribution of *Pinus caribaea* can be no older than that. In British Honduras and the interior of Honduras and Nicaragua, *P. caribaea* is found on generally poor soils formed by weathering of rocks of Paleozoic age, which tells nothing about the time span of occupancy by pines. The avifauna of the pinelands of British Honduras-Petén and the Mosquitia is sufficiently distinct from that of the interior highlands to suggest that there has never been a broad continuity between the montane pines (including *caribaea* at lower elevations) and those of the more coastal regions. On the other hand, I agree with Monroe (1968) that the presence of certain species and subspecies in both British Honduras-Petén and the Mosquitia can only be accounted for by a former continuity of pinelands between these two regions. This conclusion follows regardless of which hypothesis about the geographical and ecological origin of the lowland pine savanna one accepts.

Table 6 lists the breeding birds of the Mosquitia and the status of each of these species in pinelands in British Honduras-Petén, montane Central America, and the West Indies. The number of taxa in common are summarized.

From these data, I conclude that no species has colonized the Central American pinelands from the West Indies; that the avifauna of the Caribbean slope pinelands is largely derived from that of the montane pinelands, by fortuitous colonization but not through extensive direct connection of habitat; and that there were direct connections between the pinelands of British Honduras-Petén and the Mosquitia along the Caribbean coast which were disrupted in relatively recent times.

The avifauna of the montane pine and pine-oak forests of Honduras or Nicaragua includes the following species that are not found in the Caribbean slope pinelands: *Accipiter chionogaster*, *Otus trichopsis*, *Hylocharis leucotis*, *Eugenes fulgens*, *Trogon mexicanus*, *Colaptes auratus*, *Dendrocopos villosus*, *Cyanocitta stelleri*, *Certhia familiaris*, *Peucedramus taeniatus*, and *Myioborus pictus*. Had there been extensive direct connections between the montane and lowland pines, one would expect that at least a few of these species would be found in the latter region, either in addition to those present or in place of some of the similar species that must have reached the pines from arid scrub habitats. Most of the lowland pine species are also found in the montane pines, where they co-exist with the above-listed species that are absent from the lowlands. I have elsewhere (Howell 1971) pointed out that the lowland pine savanna is faunally impoverished but that some montane species that are absent might be expected to be resident in the lowlands had they ever reached them.

One can imagine that some species common to British Honduras-Petén and the Mosquitia could cross the several hundred miles of the entirely different habitat that presently separates the areas, but not others. Within historic times, until altered by Caucasian man, this different habitat was humid, lowland, broad-leafed forest. *Colinus nigrogularis* stands out as physically incapable of crossing such a barrier. Others unlikely to have done so which are also absent from the nearest montane pines and grasslands are *Dendrocopos scalaris*, *Pyrocephalus rubinus*, and *Aimophila botterii*. Several species are represented in both the Caribbean slope areas by the same subspecies and by a different subspecies in the montane pines. These include: *Dendroica graciae decora*, *Ammodramus savannarum cracens*, *Aimophila rufescens discolor*, and *Spizella passerina pinetorum*. These could not have been distributed through the montane pines, yet two are pine forest birds and the other two are sedentary grassland-dwellers. The evidence from bird distribution alone makes it highly probable that the pinelands of the Caribbean coastal regions were once connected.

When and by what means the connection was broken is conjectural. The break must have occurred early enough to allow sufficient isolation for the development of several different subspecies and to account for the absence of some species in one or the other area. Several species such as *Contopus pertinax*, *Cyanocorax yucatanica*, *Uropsila leucogastra*, *Mimus gilvus*, and *Vireo solitarius* are birds of the pines or pine and broad-leaf edges in British Honduras and are absent from the Mosquitia, despite the presence there of very similar habitat. More striking are the absence of *Falco sparverius* as a breeding species in British Honduras although *F. s. nicaraguensis* is a permanent resident in the Mosquitia, and the presence of the distinct subspecies *Amazilia cyanocephala chlorostephana* in the Mosquitia although the montane pines and the British Honduras pinelands are both occupied by *A. c. guatemalensis*. *Buteo jamaicensis* breeds in the Mosquitia, and its status in British Honduras-Petén is uncertain; *Capri-*

TABLE 6. Breeding birds of the Mosquitia and the distribution of these species in other pinelands.

Species and subspecies	Mosquitia	British Honduras and Petén	Montane Central America	West Indies
Buteo albicaudatus hypospodius	+	+?	+	–
Buteo jamaicensis kemsiesi	+	+?	+	–
B. jamaicensis ssp.	–	–	–	+
Polyborus plancus audubonii	+	–	–	+
Falco sparverius tropicalis	–	–	+	–
F. s. nicaraguensis	+	–	–	–
F. s. dominicensis	–	–	–	+
Falco femoralis femoralis	+?	+?	–	–
Colinus nigrogularis nigrogularis	–	+	–	–
C. n. segoviensis	+	–	–	–
Columbina minuta interrupta	+	+	+?	–
Amazona ochrocephala belizensis	–	+	–	–
A. o. parvipes	+	–	–	–
Bubo virginianus mayensis	?	+	–	–
B. v. mesembrinus	?	–	+	–
Chordeiles minor ssp.	+	+	–	–
C. m. gundlachii	–	–	–	+
Caprimulgus maculicaudus	+	–?	–?	–
Amazilia cyanocephala guatemalensis	–	+	+	–
A. c. chlorostephana	+	–	–	–
Dendrocopos scalaris leucoptilurus	+	+	local	–
Pyrocephalus rubinus blatteus	–	+	–	–
P. r. pinicola	+	–	–	–
Muscivora savana monachus	+	+	+	–
Cistothorus platensis elegans	+?	+	+	–
Sialia sialis meridionalis	–	+	+	–
S. s. caribaea	+	–	–	–
Dendroica graciae remota	–	–	+	–
D. g. decora	+	+	–	–
Icterus chrysater chrysater	+	+	+	–
Sturnella magna alticola	–	–	+	–
S. m. mexicana	–	+	–	–
S. m. inexpectata	+	–	–	–
S. m. hippocrepis	–	–	–	+
Piranga flava albifacies	–	–	+	–
P. f. figlina	–	+	–	–
P. f. savannarum	+	–	–	–
Ammodramus savannarum bimaculatus	–	–	+	–
A. s. cracens	+	+	–	–
A. s. intricatus	–	–	–	+
Aimophila rufescens rufescens	–	–	+	–
A. r. discolor	+	+	–	–
Aimophila botterii ssp.	–	–	+	–
A. b. petenica	–	+	–	–
A. b. spadiconigrescens	+	–	–	–
Spizella passerina mexicana	–	–	+	–
S. p. pinetorum	+	+	–	–
Carduelis notata oleacea	+	+	+	–
Loxia curvirostra mesamericana	+(ssp?)	+(ssp?)	+	–

Species common to Mosquitia and West Indies: 6; subspecies: 0
Species common to all three Central American regions: 19, including doubtfuls
Subspecies common to all three Central American regions: 9, including doubtfuls
Subspecies common only to B.H.-Petén and Mosquitia: 6, including doubtfuls
Subspecies of Mosquitia and B.H.-Petén populations differ: 8
Subspecies of B.H.-Petén like montane, differs from Mosquitia: 1
Subspecies of Mosquitia like montane, differs from B.H.-Petén: 0
Species resident in Mosquitia, not in B.H.-Petén: 1 certain, 2 doubtfuls

mulgus maculicaudus breeds in the Mosquitia and is unrecorded in British Honduras-Petén, but it may have been missed there because of its secretive habits.

Von Hagen (1940) suggested that very recent subsidence and flooding in the northern coast of Honduras eliminated pines in that region, but subsidence of such magnitude within historic times seems improbable. Conversely, even if the coast of Honduras and British Honduras extended out to the 100 fathom line, their extent and contours would be only slightly changed (Natl. Geogr. Soc. 1970). As previously mentioned, pine savanna in this region is replaced by broad-leafed forest unless maintained by fires. A short-term change in local climate or even a cessation of man-started fires could bring about extensive replacement of pines within a few hundred years. Bennett (1968) gives evidence that, in Panamá, great expanses of land that were cleared and burned by Indians at the time of the Spanish conquest in the 1500s had become covered with heavy forest by the late 17th century, following decimation of the aboriginal population.

The time span believed to be required for the differentiation of avian subspecies has been drastically shortened since Johnston and Selander (1964) showed that comparable differentiation has taken place in *Passer domesticus* within 50 to 100 years. Members of five different avian orders have attained subspecific distinctness in the Mosquitia, indicating a high degree of isolation of the habitat and its resident avifauna. Given such isolation and also small breeding populations, differentiation could proceed relatively rapidly. The distinctness of the avifauna, especially that of the Mosquitia, does not necessarily imply great antiquity of the habitat or its separation, and the possible influence of aboriginal man on the establishment and extent of the Caribbean pinelands cannot be ruled out although there is no direct evidence for it in pre-Columbian times. In view of these interesting uncertainties, the lowland pine savanna offers potentially rewarding possibilities for palynological and archaeological study.

I have stressed the present-day isolation of the Mosquitia from the British Honduras-Petén pinelands on the basis of published evidence, but possibly some narrow and unmapped connections exist. L. F. Kiff, who has traveled extensively in both regions, informs me that narrow belts of pinelands extend for undetermined distances into the intervening areas of broad-leafed forest. Whether these belts actually link the pinelands together and whether or not they are of very recent origin is not known. In any case, the similarities and differences in the bird faunas of the two regions seem best explained by an hypothesis of a formerly broad continuity followed by effective if not total separation of the habitats.

As expected, most of the resident species and subspecies in the lowland pine savanna have northern affinities in the sense of "a geographical relationship of a contemporary population with the region from which its present distribution was derived" (Howell 1969). Only *Buteo albicaudatus hypospodius*, *Falco femoralis femoralis*, *Caprimulgus maculicaudus*, and *Muscivora savana monachus* are likely to be of southern affinity. Each of these species inhabits open country and occurs in that type of habitat with or without pines, and the same is true of several of the resident forms of northern affinity. Pines apparently constitute a type of resource to which few bird species of tropical origin have adapted; this is particularly true of the lowland tropical pines and is consistent with an hypothesis of their recent establishment in that region.

SUMMARY

The isolated lowland pine savanna of eastern Honduras and northeastern Nicaragua (the Mosquitia) extends to the southern limit (12° 10′ N lat) of naturally occurring pines in the Western Hemisphere. Only one species of pine, *Pinus caribaea*, is present. The avifauna of the Mosquitia is distinctive, including the southernmost populations of some species of pine-adapted birds and some endemic subspecies. I review the taxonomy, distribution, and breeding status of the resident birds and also record noteworthy migrants and visitors. The resident birds are primarily of north temperate zone affinity, but a few may be of southern affinity and some are not truly pine-adapted but require habitat of open aspect as provided by the pine savanna. *Pinus caribaea* is found only from British Honduras and Petén to Nicaragua and in Cuba and the Bahamas; its closest relatives are not the pine species of México and the Central American highlands, but *Pinus elliottii* and other species of eastern North America. I suggest that *P. caribaea* reached the Caribbean coast of Central America by way of Cuba, probably in late Pleistocene or early Recent time, and that now-separated pinelands of British Honduras and the Mosquitia were once connected. The isolated Caribbean pinelands were largely and

relatively recently colonized by birds from the montane pine forests, and the British Honduras-Mosquitia continuity was even more recently disrupted. The similarities and differences of the avifaunas of the montane pines, British Honduras-Petén, and the Mosquitia are analyzed in terms of this hypothesis.

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DEDICATION

This paper is dedicated to the memory of Loye Holmes Miller—"Padre" to generations of ornithologists.

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