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OBSERVATIONS ON THE BREEDING BIOLOGY OF PASSERINES IN A SEASONALLY FLOODED SAVANNA IN VENEZUELA

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ABSTRACT.—The breeding biology of passerines was studied in a seasonally inundated savanna in the llanos of western Venezuela. A total of 412 nests of 36 species were located, and other evidence of breeding activity was observed for 13 additional species. Most species bred principally in the early half of the wet season, sometimes starting very late in the dry season. Other species bred throughout the wet season, although generally with a gradual decline in the latter half. A few species bred principally or entirely in the latter half of the wet season. Ground-nesting species bred principally, and often exclusively, at the beginning and end of the wet season, avoiding the main part of the rains. The Shiny Cowbird (*Molothrus bonariensis*) was a brood parasite on four species, with two important host species, the Pied Water-Tyrant (*Fluvicola pica*) and the White-headed Marsh-Tyrant (*Arundinicola leucocephala*). The first known nest of the River Tyrannulet (*Serpophaga hypoleuca*) and the first known breeding north of the Amazon River for the transequatorial migrant Yellow-browed Tyrant (*Satrapa icterophrys*) are described. Natural history information is presented for the little-known White-naped Xenopsaris (*Xenopsaris albinucha*), and for the Yellow-browed Sparrow (*Ammodramus aurifrons*) and the Grassland Sparrow (*A. humeralis*) in one of the few known areas of sympatry. *Received 20 May 1988, accepted 15 Sept. 1988.*

The savannas (llanos) in Colombia and Venezuela cover an area of approximately half a million km^2, constituting the largest uninterrupted surface of neotropical savanna north of the equator (Sarmiento 1984). The llanos constitute approximately a third of the surface of Venezuela, and dominate the landscape in the plains that surround the Orinoco River. The Venezuelan llanos have two dominant types: *Trachypogon* savannas (which are nearly treeless in the east and semi-wooded in the central llanos and the Andean Piedmont), and the seasonally flooded savannas in the west (Fig. 1) (Ramia 1967).

The passerine avifauna of the llanos, especially of the flooded savannas, is imperfectly known. Basic distribution and ecological information is included in Meyer de Schauensee (1964) and Hilty and Brown (1986) for Colombia, and in Phelps and Phelps (1958, 1963) and Meyer de Schauensee and Phelps (1978) for Venezuela. Species lists, with varying amounts of additional information, have been provided for the Colombian llanos by Olivares (1974), Barreto (1981), and Furniss (unpubl. data), and for the eastern and central Venezuelan llanos by Berlepsch and Hartert (1902),

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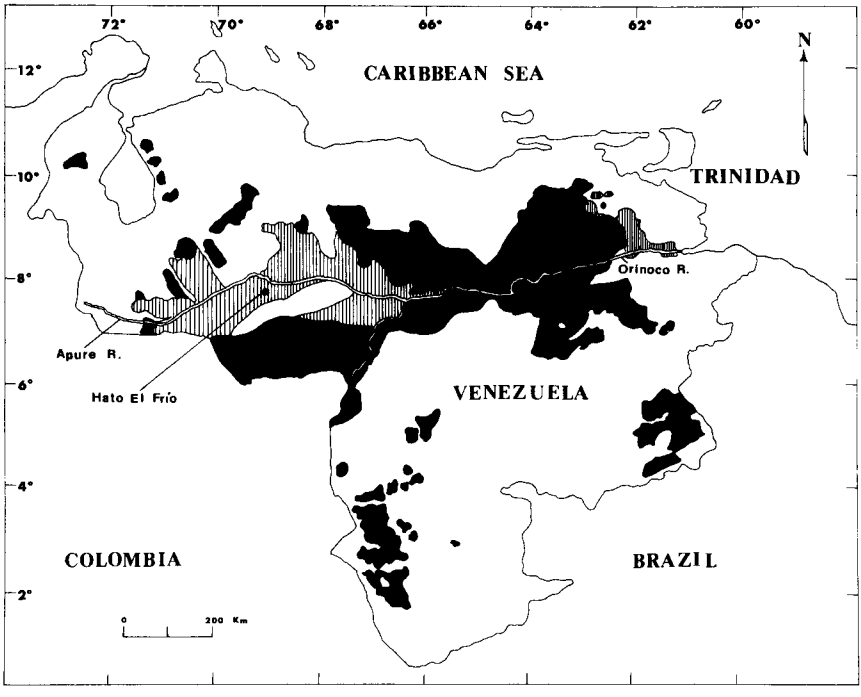

FIG. 1. Map of Venezuela showing location of the study site. Shaded areas indicate *Trachypogon* savanna, and hatched areas indicate seasonally inundated *banco-bajío-estero* savanna (adapted from Ramia 1967).

Cherrie (1916), Friedmann and Smith (1950, 1955), Smith (1952), and Thomas (1979). The only detailed passerine data for the flooded savannas of the western Venezuelan llanos are in de Visscher (1983), who examined avian community structure, principally in the isolated woodlands, and Ramo and Busto (1981, 1984), who studied breeding biology, based on 164 nests of 35 species.

In this paper, we present information on the breeding biology of 45 species, including data on 412 nests of 36 species and for the sake of completeness we also summarize the records of Ramo and Busto (1984), for a total of 54 species, and 576 nests of 48 species. We report the first known nest of *Serpophaga hypoleuca,* and the first known nest of *Satrapa icterophrys* in northern South America.

STUDY SITE

We made observations at Hato El Frío (the same site used by Ramo and Busto 1981, 1984), a cattle ranch located at 7°35'–7°55'N, 68°45'–69°00'W, in northern Apure state,

Venezuela (Fig. 1). It covers 78,000 ha at an elevation of 65–75 m. The land is flat with an east-west slope of 0.02%, and the climate is characterized by slight annual temperature variations and by well-defined rainy and dry seasons. The median annual temperature is 27°C, with a daily mean variation of 9.5°C. Temperatures vary little annually, with March the hottest month and July the coolest. At Mantecal (approx. 40 km southwest of Hato El Frío), annual precipitation varied from 1314–2080 mm, with an average of 1645 mm. About 90 percent of the rain falls in the May–October rainy season. The start of the rainy season is variable; it may be as early as late March or as late as June (Thomas 1985) or even July (pers. obs.). The December–March dry season is virtually or entirely rainless; April and November are transitional months.

Hato El Frío is situated in a flooded savanna. Most of the ranch is covered by savannas and water bodies; only about 20% is wooded. Ramia (1972) and Castroviejo and López (1980) recognized the following vegetational types on El Frío. *Matas* are isolated groves of trees 20–25 m high, with a dense shrub understory, found on sites slightly above maximum water level within an open landscape. *Gallery forests* occur along major watercourses and are subject to wet season flooding. They have a single stratum of trees 10–12 m tall. *Esteros* are alluvial bottom savannas found in depressions up to 2 m deep. They are flooded throughout the wet season and retain water into the dry season. *Caños* are riverine overflow channels which also retain water into the dry season. *Bajíos* are floodplain savannas that are shallowly flooded (up to 5 cm) only in the wet season. Their vegetation is dominated by low grasses and sedges (<15 cm). Spiny shrubs (mostly <3 m) occur sporadically, either singly or clumped. *Bancos* are riverbanks of active or former watercourses. Never flooded, they are covered by tall grass with some shrubs in different associations on the lower and higher parts. Many introduced shrubs and trees occur around buildings and on the dikes constructed for water control and/or roads.

All data were collected within a circle (diameter 4 km, area 12.6 km^2) centered on the Estación Biológica de El Frío, located beside the main complex of ranch buildings. The circle composition is approximately as follows: *banco* (mostly with human-induced disturbance communities) 25%, *estero/caño* 25%, *bajíos* 40%, and *matas* 10%. *Gallery forest* was only marginally represented. Approximately 6 km of dikes were in the area.

METHODS

Data were collected from 12 August–28 November 1982, 5 June–2 November 1983, and 28 June–7 July 1984. Nests were located by daily searches through the study area. The amount of effort in major habitat types was approximately as follows: *banco* 45%, *estero/caño* 45%, *bajíos* 10%. The nests that we located were visited regularly until no longer active. We tried to visit nests every 2–4 days, but some were checked less often. We tried to minimize the time spent at the nest and of disturbance to the surrounding vegetation. We also noted the presence or absence of eggs and nestlings of Shiny Cowbirds.

RESULTS

A total of 412 nests of 36 species were found, and behavioral evidence of breeding activity was found for an additional 13 species (Table 1). Clutch size and egg measurements are recorded in Table 2. The following species accounts amplify previous natural history observations. Detailed information is generally not included unless it is new information or augments published information.

River Tyrannulet (*Serpophaga hypoleuca*). This scarce and local species

TABLE 1

BREEDING ACTIVITY OF PASSERINES AT HATO EL FRÍO

Species	Apr	May	June	July	Aug	Sept	Oct	Nov	Total
Scardafella squammata[a]			7[b]		2	1	1	1	12
Columbina minuta[a]			5			2	1	3	11
Synallaxis albescens			4	1		3	3		11
Certhiaxis cinnamomea			11 (1)[c]	5	11	3 (1)	2 (2)		32 (4)
Cranioleuca vulpina			1 (1)	1					2 (1)
Phacellodomus rufifrons					2	1		1	4
Thamnophilus doliatus		(1)							(1)
Serpophaga hypoleuca				F[d]			1		1
Todirostrum cinereum		(6)	26 (9)	9 (3)	15	1 (1)	1		52 (19)
Tolmomyias flaviventris			1		1				2
Pyrocephalus rubinus	(4)	(2)	F		4	(1)	1		5 (7)
Fluvicola pica			23 (2)	47 (6)	24 (4)	39 (7)	11 (5)	(4)	144 (28)
Arundinicola leucocephala			3	1	3 (1)	9	3 (4)	(1)	19 (6)
Machetornis rixosus			6	1 (1)	5	2 (1)			14 (2)
Satrapa icterophrys					1	F			1
Pitangus lictor			C[d]		3	F	1		4
Pitangus sulphuratus		(2)	11 (4)	3	F				14 (6)
Myiozetetes cayanensis		(1)	4						4 (1)
Myiozetetes similis			2 (2)						2 (2)
Conopias inornata				2					2
Tyrannus melanocholicus	(1)	(1)	2	F	3	1	N[d]		6 (2)
Tyrannus dominicensis	(2)	(2)	2	F					2 (4)
Tyrannus savana							2 (1)		2 (1)
Xenopsaris albinucha			1		1	2			4

TABLE 1
CONTINUED

Species	Apr	May	June	July	Aug	Sept	Oct	Nov	Total
Pachyranphus polychopterus					1	1			2
Progne chalybea			F						
Progne tapera		(1)							(1)
Campylorhynchus griseus				(1)					(1)
Troglodytes aedon					F				
Turdus nudigenis		(1)	C						(1)
Mimus gilvus			F			(2)			(2)
Anthus lutescens		(1)				(1)	2		2 (2)
Coereba flaveola		(1)	1	C	1	1	1		4 (1)
Tangara cayana		(2)							(2)
Thraupis episcopus			(2)						(2)
Nemosia pileata							F		
Saltator coerulescens		(1)				F			(1)
Saltator orenocensis				(1)					(1)
Paroaria gularis			(1)	1	F	F			1 (1)
Volatinia jacarina				1					1
Sporophila intermedia			4 (2)		4	4 (1)	2		14 (3)
Sporophila minuta			(1)						(1)
Sicalis flaveola			7 (5)	3 (2)	4	F	(2)		14 (9)
Sicalis columbiana			F					C	
Sicalis luteola							1		1
Emberizoides herbicola			F					F	
Ammodramus aurifrons		(2)	3 (2)	(1)	2	3 (1)	5		13 (6)
Ammodramus humeralis			6				3		9

TABLE 1
CONTINUED

Species	Apr	May	June	July	Aug	Sept	Oct	Nov	Total
Agelaius icterocephalus				(1)			2		2 (1)
Gymnomystax mexicanus			C	C	C, F	F			
Sturnella militaris		(8)	(3)					(3)	(14)
Quiscalus lugubris			4 (13)	(7)		C			4 (20)
Molothrus bonariensis			16	16	9	18	10		69 (25)[e]
Icterus icterus				2					2
Icterus nigrogularis		(2)	9 (2)	7 (1)					16 (5)
Cacicus cela			(5)	(1)					(6)
Total nests (this study)			131	84	85	70	41	1	412[f]
Total nests (Ramo and Busto 1984)	7	34	55	25	5	16	14	8	164
Total nests	7	34	186	109	90	86	55	9	576[f]
Total species with nests	3	16	27	21	18	17	18	4	48

[a] Non-passerines.
[b] Nests recorded in this study.
[c] Nests recorded by Ramo and Busto (1984) in parentheses.
[d] C—nest under construction; N—food being carried to nestlings; F—dependent fledglings.
[e] Number of parasitized nests; not included in numbers of total nests.
[f] Passerines only.

TABLE 2
CLUTCH SIZES AND EGG MEASUREMENTS

	Clutch			Weight (g)			Egg dimensions (mm)			
							Length		Width	
	Range	$\bar{x}$	n[a]	Range	$\bar{x}$	n[b]	Range	$\bar{x}$	Range	$\bar{x}$
Columbina minuta	2	2.0	10				19.33–21.95	20.68	14.61–16.31	15.87
Synallaxis albescens	2–4	3.0	7	1.7–2.4	2.2	14	17.55–22.45	19.07	14.58–16.00	15.28
Certhiaxis cinnamomea	2–4	2.7	12	2.0–2.5	2.2	18	18.55–20.60	19.63	14.25–15.65	14.91
Serpophaga hypoleuca	2		1	1.0–1.1		2	14.70–14.90		11.85–11.90	
Todirostrum cinereum	2–3	2.5	12	0.80–1.6	1.2	26	15.60–17.30	16.58	11.25–12.35	11.88
Pyrocephalus rubinus	2		1	1.7–2.0		2	18.15–18.90		13.55–13.80	
Fluvicola pica	1–4	2.6	83	1.0–2.2	1.6	122	15.60–19.94	18.02	0.75–14.00	12.91
Arundinicola leucocephala	1–3	2.6	9	1.8–1.9	1.8	13	18.20–20.68	19.09	11.10–14.58	13.66
Machetornis rixosus	3		1	3.1–3.7	3.5	3	22.15–24.67	23.82	16.93–17.55	17.21
Pitangus sulphuratus	2–4	2.7	3	5.2–6.7	6.0	8	27.50–30.25	28.61	19.60–21.00	20.52
Tyrannus melancholicus	2–3	2.3	3	3.2–4.0	3.5	7	20.45–24.90	23.53	16.95–17.85	17.29
Tyrannus dominicensis	2–3	2.5	2	3.8–3.9	3.9	5	22.60–25.25	23.55	17.25–18.40	17.98
Tyrannus savana	2–3	2.5	2	2.6–3.7	3.2	5	21.55–23.50	22.53	15.35–17.35	16.51
Anthus lutescens	2–3	2.5	2	1.6–2.0	1.7	4	17.20–18.10	17.78	14.00–14.10	14.05
Paroaria gularis	2		1	2.5–2.6		2	20.40–20.75		14.95–15.05	
Sporophila intermedia	1–3	2.3	6	1.4–1.8	1.6	6	16.45–17.90	17.05	12.20–13.90	13.00
Sicalis flaveola	3–5	3.6	5	2.0–2.8	2.4	15	19.15–22.35	20.76	14.35–15.70	14.89
Sicalis luteola	3		1	1.6–1.8	1.7	3	18.00–18.85	18.38	13.80–13.95	13.88
Ammodramus aurifrons	2–3	2.4	12	1.4–2.1	1.7	13	15.50–19.30	17.64	13.70–14.86	14.35
Ammodramus humeralis	2–3	2.3	8	2.0–2.6	2.2	11	18.95–20.35	19.48	14.15–15.10	14.68

TABLE 2
CONTINUED

	Clutch			Weight (g)			Egg dimensions (mm)			
							Length		Width	
	Range	$\bar{x}$	n[a]	Range	$\bar{x}$	n[b]	Range	$\bar{x}$	Range	$\bar{x}$
Quiscalus lugubris	2–3	2.5	4	3.7–5.4	4.4	10	24.65–27.95	26.01	18.25–19.30	18.78
Molothrus bonariensis	1–4	1.6	72	2.0–4.2	3.4	80	18.70–25.35	21.92	13.75–20.09	17.35
(from *Fluvicola pica*)	1–2	1.2	56	2.0–4.2	3.3	43	18.70–23.85	21.62	13.75–18.30	17.08
(from *Arundinicola leucocephala*)	1–4	2.7	12	2.7–3.8	3.4	24	20.20–23.75	21.95	16.30–20.09	17.40
(from *Quiscalus lugubris*)	3–4	3.5	4	3.2–4.0	3.7	13	21.10–25.35	22.88	16.85–19.00	18.16
Icterus nigrogularis	2–4	3.0	5	3.6–3.8	3.8	10	24.00–25.30	24.49	16.40–17.30	16.91

Note: For some common species, egg measurements were not obtained from all clutches.
[a] Total number of clutches.
[b] Total number of eggs.

is little known, and the nest was undescribed. On 27 July 1983, a family group was observed within a *Mimosa* thicket along a dike. One member was a fledgling otherwise identical to the adults in plumage. It infrequently foraged, but usually followed the adults through the thicket, constantly begging. On 13 October 1983 at 08:40 h, we found a nest with 2 eggs. The nest was a delicate, tightly constructed cup made of fine grass with spider web woven in, especially at the points of attachment to the supporting plant. It was lined with large white feathers. The nest measured 3.5 cm from the bottom to the rim top, and 4.5 cm across the outer edges of the rim top. The cavity measured 2.7 cm deep and 3.2 cm wide. The nest was placed 55 cm above the ground in a fork between the main stem and a major side branch of an 88-cm tall *Paltea trinervis* (Malvaceae), a semi-woody herb. The plant was in the middle of a 180-m wide dry *bajío* pasture, bordered on 3 sides by dense, 2-m high thickets of *Cassia* and several scattered 7–8-m-tall trees. The 2 eggs were unmarked dull white with a very slight buffy-cream tinge (Table 2).

Pied Water-Tyrant (*Fluvicola pica*). Water-tyrants breed throughout the wet season, beginning soon after the rains start, which may be as early as late March or as late as July. In June and July 1983, 86.5% (64/74) of nests were placed adjacent to *caños* or *lagunas,* in trees, shrubs or *Mimosa piagra* thickets. As the season progressed and stiff emergent vegetation grew, nests were more often placed within such vegetation in *esteros* (84.4% in September and October).

White-headed Marsh-Tyrant (*Arundinicola leucocephala*). The species breeds throughout the wet season, with a peak in the latter half of the season (15 of 19 nests in August–October). As with *F. pica,* early (June–July) nests were near *caños* and *lagunas* (100%, N = 4), while late (September–October) nests were in *esteros* (100%, N = 15).

Yellow-browed Tyrant (*Satrapa icterophrys*). It was uncommon in semi-open *bancos,* mostly near water. This species breeds during October–December from northeastern and central Brazil and northern Bolivia to Northern Argentina and migrates north across the equator to spend the austral winter in Venezuela (Meyer de Schauensee 1966, Meyer de Schauensee and Phelps 1978). We recorded 2 cases of confirmed breeding at Hato El Frío. On 17 August 1982, a pair was observed constructing a nest. On 21 August, it appeared complete but it had no lining when we examined it. The nest was a shallow cup of fine twigs and rootlets with some untidy strands of material hanging below. The nest was placed 2 m above ground in a distal fork of a branch of a 20–25-m-tall *Ceiba pentandra.* The nest subsequently disappeared, perhaps due to the activity of a pair of *Phacellodomus rufifrons,* which constructed a nest at the precise spot where the tyrant nest had been.

At 08:00 h on 21 September 1983, two recently fledged dependent juveniles were observed in a thicket bordering a small laguna. They perched together low in the shrubbery, only occasionally attempting short, clumsy flights. They did not move about or follow the adults, and their begging was generally restrained. The young birds were about ¾ adult size, with very short bills and stubby tails. All four birds were seen at the same spot on 26 September, but not thereafter.

White-naped Xenopsaris (*Xenopsaris albinucha*). Uncommon in *bancos,* with scattered trees, shrubs, and tall herbaceous vegetation. Nests were found through most of the wet season (June–September). All were cups placed in forks between branches 10–15 m high in trees 15–20 m tall. Sitting birds were seen on these nests on 23 and 28 August.

Saffron Finch (*Sicalis flaveola*). Nest were placed in nests of *Certhiaxis cinnamomea* (8), *Phacellodomus rufifrons* (7), *Icterus nigrogularis* (5), 1 each in nests of *Fluvicola pica, Pitangus sulphuratus* and *Cacius cela,* and 1 in a hole in a wooden fence-post. Man-made structures such as buildings, stone walls, and hollow pipes have also been used (Friedmann and Smith 1950, C. Casler pers. comm.).

Yellow-browed Sparrow (*Ammodramus aurifrons*) and Grassland Sparrow (*A. humeralis*). The distribution of these species is generally allopatric; *aurifrons* occurs mainly in the Amazon basin (especially the western half), and *humeralis* is found widely both north and south of the Amazon basin (Short 1975). At El Frío, both species were found, *aurifrons* much more commonly. Their distribution overlapped widely but only *humeralis* was found in *bajíos* (except at the borders between *bajíos* and *bancos,* where both species were found). In general *aurifrons* was found in areas with more shrubs and scattered trees, while *humeralis* preferred more open areas such as *bajíos* and grassy *bancos.* Most *aurifrons* nests were found in grassy-herbaceous sites on *bancos,* while most *humeralis* nests were in *bajíos* (either wet or dry), but they were generally widely separated. In other areas of sympatry either the two species showed complete habitat segregation or only one of the two species was present locally.

Yellow-hooded Blackbird (*Agelaius icterocephalus*). Two solitary nests recorded at El Frío were unusual for this normally highly social species. At Hato Masaguaral, Wiley and Wiley (1980) recorded nesting only in a 6-week period from mid-October to late November; however, they do not nest there every year (B. T. Thomas pers. comm.). At Masaguaral, blackbirds nested only in stands of *Thalia,* a tall, stiff emergent, aquatic plant. Prior to October, the plants were not large enough to support nests, and by late November, the wet areas were dry or rapidly drying, and the plants were decaying. The July nest at El Frío was in the grass *Paspalum fasciculatum* in an *estero,* and the October nest was in a small (60 m^2)

stand of *Thalia* in an *estero.* The absence of *Thalia* stands or similar dense, robust emergent vegetation in the study area probably accounts for the rarity of this species.

Shiny Cowbird (*Molothrus bonariensis*). This widespread species is a brood parasite, with records of parasitism on 201 species (Friedmann and Kiff 1985). Seven passerine species were found to be parasitized at Hato El Frío (4 in this study, and 6 by Ramo and Busto 1980, 1981); four species were important hosts. The 7 species were: 1. *Cranioleuca vulpina.* Ramo and Busto found 1 parasitized nest, and 1 parasitized nest had been observed previously (in Venezuela) by Cherrie (1916). 2. *Fluvicola pica.* Ramo and Busto recorded an 11% rate of parasitism (3 of 27), whereas 54 of 102 (54%) nests that we found were parasitized. 3. *Arundinicola leucocephala.* Rates of parasitism at Hato El Frío were very high: 80% (4 of 5 nests) by Ramo and Busto and 92% (12 of 13 nests) in this study. 4. *Campylorhynchus griseus.* One parasitized nest was found by Ramo and Busto, and 1 case was recorded at Masaguaral (Thomas in Friedmann and Kiff 1985). 5. *Agelaius icterocephalus.* Three nests have been found at El Frío: 1 unparasitized nest by Ramo and Busto, and 1 unparasitized and 1 parasitized nest by us. 6. *Sturnella militaris.* Ramo and Busto found that 71% (10 of 14) of the nests were parasitized, all early in the breeding season (May–June). 7. *Quiscalus lugubris.* Ramo and Busto found 30% (6 of 20) of nests parasitized. All four nests we found had been parasitized; all had been abandoned when found.

DISCUSSION

Savannas appear to be one of the most marked examples of seasonal tropical ecosystems with rainfall concentrated in 4–6 months, and a dry season of no less than 4 months with little or no rain. The contrast between the periods of rain and drought is marked. The landscape at Hato El Frío changes accordingly; in the wet season much of the land is flooded, at least shallowly, with only small and widely scattered (and mostly man-made) areas remaining above water, while in the dry season it has an arid appearance, with the little remaining water highly concentrated in a few watercourses, *esteros,* and man-made stock ponds. The annual cycles of plants and animals are consequently highly seasonal.

In seasonal areas of the tropics, passerines are primarily wet season breeders (Skutch 1950, Snow and Snow 1964, Fry 1983). At Hato Masaguaral, only 3 of 54 species of breeding passerines are known to nest exclusively in the dry season (Thomas 1979), although an additional 8 species started breeding in the late dry season and continued into the wet season. Even within the wet season, breeding activity is not evenly distributed. Breeding activity at El Frío showed a peak in the first half of

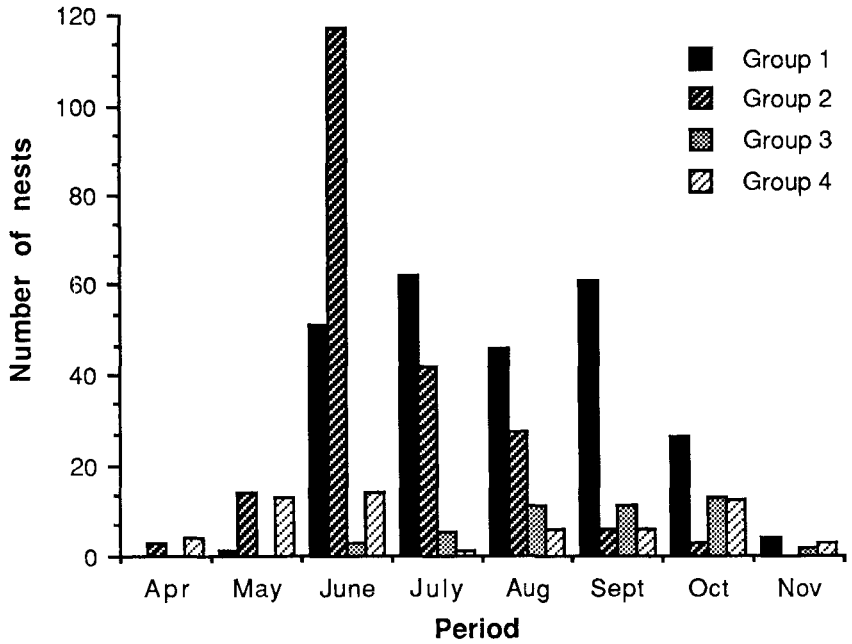

FIG. 2. The breeding chronology of passerines in the Venezuelan llanos (see text for species in each group).

the wet season, then dropped to a lower level in the second half before virtually ending in November (Fig. 2). Both our data and those of Ramo and Busto (1984) show the same pattern.

Although the avifauna as a whole bred throughout the wet season, individual species showed different peak breeding periods within the wet season. We have grouped 42 species according to peak breeding times in the llanos. These periods are based principally on data from Hato El Frío (Ramo and Busto 1984, this study) and Hato Masaguaral, 170 km to the northeast in an area of semiwooded *Trachypogon* savanna (Thomas 1979, pers. comm.). The El Frío data were collected from April to mid-December in 3 years, and presented as number of nests by month (Table 1). The records from Masaguaral, collected in all months over a period of 6 years, give the months when a species was found breeding, but not the number of nests. The breeding season patterns observed were as follows:

Group 1. Through most of the wet season, with a decrease in the late wet season (Fig. 2): *Synallaxis albescens, Certhiaxis cinnamomea, Tolmomyias flaviventris, Fluvicola pica, Xenopsaris albinucha, Troglodytes aedon, Coereba flaveola, Paroaria gularis, Sporophila intermedia, Mol-*

othrus bonariensis, and *Icterus icterus*—(11 species, 26.2%). A brief decrease apparently occurs in the middle of the wet season for at least some species (*Synallaxis albescens, Fluvicola pica*).

Group 2. Mainly in first half of the wet season (June peak), with many or most beginning to breed very late in the dry season (March or April) and some breeding in small numbers in the second half (Fig. 2): *Cranioleuca vulpina, Todirostrum cinereum, Machetornis rixosus, Pitangus sulphuratus, Myiozetetes cayanensis, M. similis, Conopias inornata, Tyrannus melancholicus, T. dominicensis, Campylorhynchus griseus, Thraupis episcopus, Sicalis flaveola, Quiscalus lugubris, Icterus nigrogularis, Gymnomystax mexicanus,* and *Cacicus cela*—(16 species, 38.1%).

Group 3. Second half of the wet season (August–October), sometimes with sporadic or much lower levels of activity in the first half (Fig. 2): *Phacellodomus rufifrons, Arundinicola leucocephala, Satrapa icterophrys, Pitangus lictor, Tyrannus savana, Pachyramphus polychopterus, Volatinia jacarina,* and *Agelaius icterocephalus*—(8 species, 19.0%).

Group 4. Bimodal, breeding at the start (May–June) and end (August–October) of the wet season, sometimes with limited numbers during the middle of the wet season (Fig. 2): *Pyrocephalus rubinus, Anthus lutescens, Ammodramus aurifrons, A. humeralis, Sturnella militaris, Sicalis luteola,* and *Emberizoides herbicola*—(7 species, 16.7%). With the exception of *P. rubinus,* these species breed on or near the ground in or near *bajíos,* and they nest either before the *bajíos* become flooded or after they have begun to dry out.

Data from Hato Masaguaral (Thomas 1979) and Carimagua, in Meta, Colombia (Furniss, unpubl. data) indicate that *Mimus gilvus* and *Sicalis columbiana* breed in late dry to early wet season (February–June) and that *Campostoma obsoletum* and *Tachycineta albiventer* breed in the dry season (December–February).

Since the optimal period for reproduction is that when food is most abundant, it is not surprising that most of the birds in the llanos and other seasonal areas of the tropics breed in the wet season, when they exploit the seasonal flush of vegetation, insects, and other food then available (Immelmann 1971, Fry 1983). Seasonal fluctuations in tropical insect populations have been documented in a number of studies, including the llanos (Wolda 1978, Travieso et al. 1977). Insect biomass increases with plant productivity and standing crop biomass. The lower insect biomass values are found during the dry season, whereas peak values are reached during the wet season.

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