



## BREEDING SEASON AND CLUTCH SIZE OF BIRDS AT SAPUCÁI, DEPARTAMENTO PARAGUARÍ, PARAGUAY

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**Resumen.-** Se presentan datos sobre la estación de nidificación y tamaño de la camada de 63 especies de aves en Sapucái, Departamento Paraguari, Paraguay, basados en 454 camadas de huevos en colecciones de museos. La colección de huevos representa solamente 30% de las especies de aves colectadas en Sapucái y que presumiblemente nidifican allí. Todos los huevos fueron colectados entre los meses de septiembre y febrero; durante los meses de octubre y noviembre, que representan el pico de nidificación, se registró la nidificación de aproximadamente 2/3 de las especies. Se examinaron cuatro variables (grupo taxonómico, tipo de nido construido, tamaño del cuerpo, y movimientos anuales) que potencialmente afectaron la estación de reproducción (cantidad de especies que nidifican por mes, fecha temprana de huevos, fecha última de huevos y duración de nidificación) y la productividad reproductiva (tamaño de la camada) de las aves de Sapucái. La única variable asociada significativamente con la estación de reproducción o la productividad reproductiva fue el tamaño del cuerpo, que fue correlacionado positivamente con el tamaño de la camada de las aves no-paserinas. Se necesitan más datos de varias localidades de América del Sur para probar mejor las hipótesis acerca de la significancia adaptativa de la estación de nidificación y la variación del tamaño de la camada.

**Palabras clave:** *movimientos anuales, tamaño corporal, temporada de cría, tamaño de nidada, tipo de nido, Paraguay, Sapucái.*

**Abstract.-** I present data on the breeding season and clutch size of 63 species of birds at Sapucái, Departamento Paraguari, Paraguay, based on 454 clutches of eggs in museum collections. The egg collections represent only 28.5% of the bird species collected at Sapucái and presumed to breed there. All eggs were collected between the months of September and February; roughly two-thirds of the species were recorded breeding during October and November, which represent the breeding peak. I examined four variables (taxonomic group, type of nest constructed, body size, and annual movements) that potentially affected the timing of reproduction (number of species incubating per month, early egg date, late egg date, and duration of breeding) and reproductive output (clutch size) by birds at Sapucái. The only variable significantly associated with the timing of reproduction or reproductive output was body size, which was positively correlated with clutch size for non-passerines. More data are needed from a variety of South American localities to accurately test hypotheses regarding the adaptive significance of the timing of breeding and variation in clutch size.

**Key words:** *annual movements, body size, breeding season, clutch size, nest type, Paraguay, Sapucái.*

Much remains to be learned about the factors affecting the breeding season and clutch sizes of birds in South America. Several studies have compiled and analyzed data on the breeding season and clutch size of landbird communities at specific localities in Venezuela (Cruz & Andrews 1989, Poulin et al. 1992, Tarroux & McNeil 2003), Trinidad and Tobago (Snow & Snow 1964, Hayes & Samad 2002), Ecuador (Marchant 1959, 1960), Brazil (Davis 1945, Prattelli et al. 2000, Marini & Durães 2001, Mallet-Rodrigues 2005, Repenning & Fontana 2011, Johnson et al. 2012, Marini et al. 2012, Stouffer et al. 2013), and Argentina (Mason 1985, de la Peña 1995, Mezquida & Marone 2001, Auer et

al. 2007). In most of these studies the seasonality of breeding was inferred from the reproductive condition (brood patch or gonad size) of banded birds or collected specimens rather than actual observations of nests, eggs, or chicks, with no data provided on clutch size.

More precise information on the reproductive activities of birds in various geographical areas is needed to more rigorously test hypotheses regarding the adaptive significance of the timing of reproduction (e.g., Lack 1968, Ricklefs 1969, Perrins 1970, Daan et al. 1988, Keast 1990, Yom-Tov 1992) and variation in clutch size (e.g., Cody 1966, Klomp 1970, Ricklefs 1970, Foster 1974, Snow 1978, Slagsvold

1982, Winkler & Walters 1983, Murray 1985, Saether 1985, Kulesza 1990, Yom-Tov et al. 1994, Böhning-Gaese et al. 2000, Martin et al. 2000, Styrsky et al. 2005, Auer et al. 2007). Basic information on the breeding distribution of South American birds is required to better understand the seasonal distribution of migrant and non-migrant birds (e.g., Sick 1968, Willis 1988, Chesser 1994, 1998, Hayes et al. 1994, Hayes 1995a, Chesser & Levey 1998, Jahn et al. 2004, 2012) and for testing historical and ecological hypotheses of bird distribution (e.g., Beven et al. 1984, Haffer 1985, 1987, Cracraft & Prum 1988, Gotelli & Graves 1990, Hayes 1995a).

In the Republic of Paraguay, which straddles the Tropic of Capricorn in the interior of South America, there is a paucity of information on the breeding biology of birds (Hayes 1995a, Guyra Paraguay 2004). Two of the earlier papers on Paraguayan ornithology reported a fair amount of data on nesting in southern Paraguay (Dalgleish 1889, Chubb 1910). Steinbacher (1962) inferred the breeding seasons of birds in the central Chaco of western Paraguay by the subjective evaluations of ovary size on specimen labels. De la Peña (2010) described the nests, eggs, and breeding season of each species in Paraguay. Anecdotal reports of nesting are scattered in the literature. Thus far there have been no attempts to quantify the clutch size or breeding season of birds at any locality in Paraguay.

In this paper I summarize data on the breeding season, extreme egg dates, and clutch size of 63 species of birds, based on museum egg collections obtained from a humid forest locality in southern Paraguay. I examine sampling bias in the egg collection and test the hypotheses that the timing of breeding and clutch size of an avifauna at a single locality are related to taxonomic group, type of nest constructed, body size, and annual movements.

## METHODS

**STUDY AREA:** From 1900–1908, the British immigrant William T. Foster collected bird eggs at

Sapucái (Sapucay in earlier literature; Paynter 1989), Departamento Paraguairí, in southern Paraguay. This subtropical locality, situated at 25°40'S, 56°55'W with an altitude of about 220 m (Paynter 1989), was originally covered by humid deciduous forest typical of the upper Paraná River basin and southeastern Brazil (Esser 1982, Hayes 1995a). Nearly all of the humid forest at the locality has been subsequently cleared (Esser 1982), but a large tract of mature humid forest with a similar avifauna remains at nearby Parque Nacional Ybycuí, only 45 km to the south-southeast, in Departamento Paraguairí (Hayes & Scharf 1995). The humid forest once present at Sapucái represented the westernmost extension of this forest as well as the westernmost limit for many species of humid forest birds in Paraguay (Hayes 1995a). Annual temperatures at Sapucái average about 22°C and annual precipitation averages about 1500 mm (Anonymous 1985, Hayes 1995a).

**BREEDING DATA:** I obtained data from the entire Sapucái egg collection at the National Museum of Natural History (USNM) in Washington, DC, USA, which I examined and compared with a printout from the computerized catalog. I obtained data photocopied from the original catalog for the entire Sapucái egg collection at the Natural History Museum (BMNH) in London, UK, but was unable to examine the collection to verify the accuracy of the data. However, Chubb (1910) reported much, but not all, of the data from the BMNH collection. When discrepancies occurred (rarely) in the data (usually dates) between Chubb (1910) and the BMNH catalog, I chose the latter as being correct. The data for the two collections were combined. In both collections, data were excluded for several clutches in which the species identification was indicated (on the labels or in the catalog) as uncertain (e.g., *Turdus* sp.) or unknown, except for *Molothrus* sp. For all other clutches the identifications were assumed to be correct.

To determine what proportion of the avifauna is represented by the egg collection, I compiled

a list of species collected at Sapucái during the same time period, based on published records in Oberholser (1902) and Chubb (1910), specimens personally examined in the USNM and the American Museum of Natural History (AMNH) in New York, New York, USA, and the online catalog of the University of Michigan Museum of Zoology (UMMZ) in Ann Arbor, Michigan, USA. The potential breeding status of each species at Sapucái was evaluated by data on the seasonal distribution of birds in Paraguay (Hayes et al. 1994, Hayes 1995a, Guyra Paraguay 2004). The taxonomy and sequence of species follow Remsen et al. (2014).

**REPRODUCTIVE MEASURES:** Four measures were used for the timing of reproduction: (1) number of species incubating per month; (2) early egg date; (3) late egg date; and (4) duration of incubation, defined as the difference between early and late egg dates. The number of species breeding each month included months within extreme dates of a given species even though no clutches were collected. To facilitate statistical comparisons, early and late egg dates were transformed into numbers with the month being a whole number (beginning with nine for September) and the day being a fraction ( $[\text{day} - 1] / x$  days during month) so that the first day of the month would have a fraction of zero (e.g., 1 October = 10.0); the months of January and February, being at the end of the breeding season, were given whole number values of 13 and 14, respectively, and February dates were calculated using 28 days.

Reproductive output was measured by clutch size, defined as the mean number of eggs per nest for each species. Undoubtedly some of the clutches from the Sapucái collections were incomplete; thus, the mean clutch size for some species may be an underestimate of the actual clutch size. However, data from egg collections of noncolonial birds are generally unbiased when compared with data from field studies (e.g., McNair 1985, 1987). Although some of the clutches may have been produced by the

same female, each clutch was assumed to be independent. Data for group-nesting species (i.e., species in which clutches from more than one female are laid in a single nest), including Smooth-billed (*Crotophaga ani*) and Guira Cuckoo (*Guira guira*), and data for brood parasitic species (i.e., species laying eggs in broods of other birds), including Shiny Cowbird (*Molothrus bonariensis*), were excluded from the analyses of clutch size.

I examined four variables that potentially affect the timing of reproduction and reproductive output: taxonomic group, type of nest constructed, body size, and annual movements.

**TAXONOMIC GROUP:** The birds were divided into three broad taxonomic groups for comparisons: (1) non-passerines; (2) suboscine passerines; and (3) oscine passerines (Sibley and Ahlquist 1990).

**TYPE OF NEST:** The birds were divided into four groups based on the type of nest most frequently constructed: (1) ground nests, made on the surface of the ground; (2) cup nests, made of vegetational matter and placed above the ground; (3) cavity nests, in the ground or a tree; and (4) enclosed nests, made of vegetation or mud. Data on the type of nest typically constructed by each species were obtained from de la Peña (1987, 2010) and Sick (1993), with the caveat that individual variation occurs in some species.

**BODY SIZE:** Body mass is generally considered to be the best univariate measure of body size (e.g., Rising & Somers 1989, Freeman & Jackson 1990) and the most readily available (Dunning 1992). Data on mean body mass, averaged between the sexes, on birds in Paraguay were obtained primarily from Storer (1989); additional data on birds occurring in Paraguay, but obtained from other countries, were obtained from Dunning (1992). To minimize the potential effects of body mass variability (e.g., Clark 1979), I placed each breeding species into one of ten non-overlapping body size classes, with each

successive body size class being approximately 1.5 times larger than the previous one (Gotelli & Graves 1990, Hayes 1995a): 1 = 0-10 g; 2 = 10-25 g; 3 = 25-47 g; 4 = 47-81 g; 5 = 81-130 g; 6 = 130-204 g; 7 = 204-314 g; 8 = 314-479 g; 9 = 479-726 g; 10 = >726 g. The accuracy of placement into a given body size class should be  $\pm 1$ .

**ANNUAL MOVEMENTS:** The breeding birds were divided into two groups based on their annual movements: (1) Neotropical austral migrant species (Hayes 1995b), which are known to migrate long distances northward after breeding; and (2) non-migrant species, which are not known to migrate long distances. Data on the annual movements of birds were based on analyses of the seasonal distribution of birds in Paraguay (Hayes et al. 1994, Hayes 1995a, Guyra Paraguay 2004).

**STATISTICAL ANALYSES:** To determine whether sampling bias occurred among the number of species belonging to different taxonomic groups, a chi-square test ( $\chi^2$  statistic; Zar 1999) was used to compare the proportion of species represented in the egg collection compared with species represented in the skin collection for all three groups. To determine whether the number of clutches collected per species varied among species belonging to the different taxonomic and nest-type groups, respectively, Kruskal-Wallis tests ( $H$  statistic; Zar 1999) and a posteriori multiple comparison tests were computed. Sampling bias between migrant and non-migrant birds was evaluated with a Mann-Whitney  $U$  test. Sampling bias among birds belonging to different body size categories was evaluated with a Spearman rank correlation coefficient ( $r_s$  statistic; Zar 1999).

To evaluate whether the reproductive measures of early egg date, late egg date, duration of incubation, and clutch size were correlated with sample size, Spearman rank correlation coefficients were computed to compare each reproductive measure with the number of clut-

ches per species.

Chi-square tests were used to compare seasonal differences among birds belonging to the different taxonomic groups and nest-type groups, respectively. Kruskal-Wallis tests were used to compare early egg date, late egg date, duration of incubation, and clutch size among species belonging to the different taxonomic groups and nest-type groups, respectively.

Variation in body size among birds belonging to different taxonomic and nest-type groups, respectively, was evaluated with Kruskal-Wallis tests. Spearman rank correlation coefficients were used to evaluate the effect of body size on the reproductive measures of early egg date, late egg date, duration of incubation, and clutch size, respectively. Bartlett's test for equality of variances ( $F$  statistic; Zar 1989) was used to compare variation in body size between non-passerines and passerines.

A Mann-Whitney  $U$  test was used to compare clutch size between migrant and non-migrant species of birds. Sample sizes were too small to permit comparisons of reproductive timing between migrant and non-migrant species.

All statistical tests were computed with Statistix 9 software (Anonymous 2008).

## RESULTS

**FAUNAL COMPOSITION:** Eggs from 454 clutches, representing at least 63 species of birds, were identified in the collections (Table 1). Foster (*in* Chubb 1910) reported an additional four species of birds known to nest at Sapucái. These included White-barred Piculet (*Picumnus cirratus*), Yellow-fronted Woodpecker (*Melanerpes flavirostris*; nestling seen on 5 November), Blue-billed Black-Tyrant (*Knipolegus cyanirostris*; BMNH clutch with four eggs, two apparently from a parasite, but identification questioned by Hayes et al. [1994]), and Brown-crested Flycatcher (*Myiarchus tyrannulus*). Thus, at least 66 species of birds (excluding the Blue-billed Black-Tyrant) have been recorded breeding at Sapucái.

Of the 233 species of birds collected at

**Table 1.** Number of clutches per month, extreme egg dates, clutch sizes and types of nests for birds collected at Sapucái, Departamento Paraguari, Paraguay.

Species	Number of Clutches <sup>a</sup>						Extreme Egg Dates <sup>b</sup>		Clutch Size				Nest type <sup>c</sup>
	S	O	N	D	J	F	Early	Late	$\bar{X}$	SD	Range	<i>n</i>	
Solitary Tinamou <i>Tinamus solitarius</i>	–	1	2	–	–	–	10-04	11-26	2.7	0.6	2–3	3	Gr
Small-billed Tinamou <i>Crypturellus parvirostris</i>	–	–	2	3	–	–	11-17	12-21	5.2	1.1	4–8	11	Gr
Tataupa Tinamou <i>Crypturellus tataupa</i>	–	1	4	3	–	–	10-01	12-17	3.8	0.7	3–5	8	Gr
Red-winged Tinamou <i>Rhynchotus rufescens</i>	–	1	2	2	1	–	10-04	01-03	2.4	0.6	1–5	8	Gr
Spotted Nothura <i>Nothura maculosa</i>	–	–	2	1	–	–	11-25	12-03	3.3	1.7	1–5	4	Gr
Bicolored Hawk <i>Accipiter bicolor</i>	–	1	–	–	–	–	10-18	10-18	3.0	–	3	1	Cu
Southern Lapwing <i>Vanellus chilensis</i>	–	3	–	–	–	–	10-03	10-17	2.8	1.0	2–4	4	Gr
South American Snipe <i>Gallinago paraguaiiae</i>	–	1	2	2	1	–	10-16	01-07	2.3	0.5	2–3	6	Gr
Pale-vented Pigeon <i>Patagioenas cayennensis</i>	–	–	7	5	1	–	11-05	01-09	2.0	0.0	2	15	Cu
White-tipped Dove <i>Leptotila verreauxi</i>	–	7	2	–	–	–	10-03	11-29	2.0	0.0	2	11	Cu
Ruddy Ground-Dove <i>Columbina talpacoti</i>	–	1	6	3	2	2	10-10	02-13	1.8	0.4	1–2	14	Cu
Smooth-billed Ani <i>Crotophaga ani</i>	–	–	6	6	–	–	11-07	12-21	16.9	6.4	10–36	14	Cu
Guira Cuckoo <i>Guira guira</i>	–	1	5	–	1	–	10-29	01-04	11.0	0.6	5–17	9	Cu
Tropical Screech-Owl <i>Megascops choliba</i>	–	4	–	–	–	–	10-04	10-20	2.3	0.5	2–3	4	Ca
Nacunda Nighthawk <i>Chordeiles nacunda</i>	–	3	–	–	–	–	10-03	10-14	1.7	0.6	1–2	3	Gr
Common Pauraque <i>Nyctidromus albicollis</i>	–	5	–	–	–	–	10-09	10-22	2.0	0.0	2	5	Gr
Little Nightjar <i>Setopagis parvula</i>	–	1	1	–	–	–	10-12	11-18	2.0	0.0	2	2	Gr
Gilded Sapphire <i>Hylocharis chrysura</i>	–	–	–	1	–	–	12-17	12-17	2.0	1.4	1–3	2	Cu

<sup>a</sup>Letters denote the months of September–February<sup>b</sup>Month-day<sup>c</sup>Bp = brood parasite; Ca = cavity; Cu = cup; En = enclosed; Gr = ground (see Methods for definitions)



**Table 1 (continued).** Number of clutches per month, extreme egg dates, clutch sizes and types of nests for birds collected at Sapucái, Departamento Paraguari, Paraguay.

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	S	O	N	D	J	F	Early	Late	$\bar{X}$	SD	Range	<i>n</i>	
Green-barred Woodpecker <i>Colaptes melanochloros</i>	–	1	–	–	–	–	10-24	10-24	1.0	–	1	1	Ca
Campo Flicker <i>Colaptes campestris</i>	–	1	–	–	–	–	10-12	10-12	4.0	–	4	1	Ca
Lineated Woodpecker <i>Dryocopus lineatus</i>	–	2	–	–	–	–	10-10	10-23	3.0	0.0	3	2	Ca
American Kestrel <i>Falco sparverius</i>	–	–	1	–	–	–	11-29	11-29	4.0	–	4	1	Ca
Rufous-breasted Leaftosser <i>Sclerurus scansor</i>	–	–	1	–	–	–	11-12	11-12	2.0	–	2	1	Ca
Great Rufous Woodcreeper <i>Xiphocolaptes major</i>	–	–	–	–	–	–	–	–	3.0	–	3	1	Ca
Rufous Hornero <i>Furnarius rufus</i>	–	2	–	–	–	–	10-10	10-12	3.0	0.0	3	2	En
Firewood-Gatherer <i>Anumbius annumbi</i>	–	1	–	–	–	–	10-16	10-16	5.0	–	5	1	En
Chotoy Spinetail <i>Schoeniophylax phryganophilus</i>	–	2	2	–	–	–	10-16	11-25	3.0	1.9	1–6	5	En
Yellow-bellied Elaenia <i>Elaenia flavogaster</i>	–	–	7	5	1	–	11-08	01-01	1.6	0.5	1–2	13	Cu
Sepia-capped Flycatcher <i>Leptopogon amaurocephalus</i>	–	1	–	–	–	–	10-13	10-13	2.0	–	2	1	En
Yellow-olive Flycatcher <i>Tolmomyias sulphurescens</i>	–	1	–	–	–	–	10-20	10-20	3.0	–	3	1	En
Gray Monjita <i>Xolmis cinereus</i>	–	1	–	–	–	–	10-16	10-16	3.0	–	3	1	Ca
Streamer-tailed Tyrant <i>Gubernetes yetapa</i>	–	–	–	1	–	–	12-03	12-03	3.0	–	3	1	Cu
Cattle Tyrant <i>Machetornis rixosa</i>	–	1	3	1	–	–	10-11	12-01	2.0	1.0	1–3	5	Ca
Piratic Flycatcher <i>Legatus leucophaeus</i>	–	–	1	–	–	–	11-23	11-23	2.0	–	2	1	En
Great Kiskadee <i>Pitangus sulphuratus</i>	–	3	10	2	1	–	10-11	01-02	2.8	1.0	1–4	17	En
Streaked Flycatcher <i>Myiodynastes maculatus</i>	–	–	1	–	–	–	11-22	11-22	2.0	–	2	1	Ca

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	S	O	N	D	J	F	Early	Late	$\bar{X}$	SD	Range	<i>n</i>	
Boat-billed Flycatcher <i>Megarynchus pitangua</i>	–	1	1	–	1	–	10-12	01-01	3.3	0.6	3–4	3	Cu
Tropical Kingbird <i>Tyrannus melancholicus</i>	–	–	4	–	–	–	11-04	11-27	2.5	0.6	2–3	4	Cu
Fork-tailed Flycatcher <i>Tyrannus savana</i>	–	1	31	2	–	–	10-13	12-04	3.1	0.9	1–5	36	Cu
Short-crested Flycatcher <i>Myiarchus ferrox</i>	–	3	5	2	–	–	10-10	12-20	3.0	0.7	2–4	10	Ca
Swallow-tailed Manakin <i>Chiroxiphia caudata</i>	–	–	1	–	–	–	11-19	11-19	2.0	–	2	1	Cu
Green-backed Becard <i>Pachyramphus viridis</i>	–	1	–	–	–	–	10-12	10-12	3.0	–	3	1	En
Red-eyed Vireo <i>Vireo olivaceus</i>	–	–	1	–	–	–	11-11	11-11	3.0	–	3	1	Cu
Purplish Jay <i>Cyanocorax cyanomelas</i>	–	9	6	1	1	–	10-01	01-05	3.2	1.2	2–5	19	Cu
Plush-crested Jay <i>Cyanocorax chrysops</i>	–	11	5	4	–	–	10-01	12-17	2.6	0.8	2–4	20	Cu
Gray-breasted Martin <i>Progne chalybea</i>	–	–	1	–	–	–	11-05	11-05	4.0	–	4	1	Ca
House Wren <i>Troglodytes aedon</i>	1	6	16	10	1	1	9-23	02-07	3.3	1.1	1–6	35	Ca
Pale-breasted Thrush <i>Turdus leucomelas</i>	–	1	3	7	–	–	10-03	12-23	2.4	0.5	2–3	11	Cu
Rufous-bellied Thrush <i>Turdus rufiventris</i>	2	4	5	2	–	1	9-29	02-06	2.5	1.0	1–4	13	Cu
Creamy-bellied Thrush <i>Turdus amaurochalinus</i>	–	5	5	1	1	–	10-09	01-02	2.9	0.7	2–4	12	Cu
Sayaca Tanager <i>Thraupis sayaca</i>	–	1	10	4	–	–	10-08	12-27	2.1	0.7	1–3	17	Cu
Wedge-tailed Grass-Finch <i>Emberizoides herbicola</i>	–	1	2	–	–	–	10-30	11-21	4.3	1.2	3–5	3	Cu
Great Pampa-Finch <i>Embernagra platensis</i>	–	–	2	–	–	–	11-08	11-08	3.0	1.4	2–4	2	Cu
Red-crested Finch <i>Coryphospingus cucullatus</i>	–	3	11	10	1	1	10-07	02-03	2.5	0.5	2–3	26	Cu

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	S	O	N	D	J	F	Early	Late	$\bar{X}$	SD	Range	<i>n</i>	
Rufous-collared Sparrow <i>Zonotrichia capensis</i>	–	5	6	7	3	–	10-07	01-17	2.7	0.6	2–4	24	Cu
Grassland Sparrow <i>Ammodramus humeralis</i>	–	1	4	–	–	–	10-08	11-22	2.2	0.4	2–3	5	Gr
Masked Yellowthroat <i>Geothlypis aequinoctialis</i>	–	–	5	–	–	–	11-05	11-27	2.4	0.5	2–3	5	Cu
Golden-crowned Warbler <i>Basileuterus culicivorus</i>	–	–	1	–	–	–	11-23	11-23	2.0	–	2	1	Gr
Variable Oriole <i>Icterus pyrrhopterus</i>	–	1	–	1	–	–	10-31	12-11	3.5	2.1	2–5	2	En
Chopi Blackbird <i>Gnorimopsar chopi</i>	–	1	4	2	–	–	10-31	12-06	3.0	1.4	1–5	7	Ca
Yellow-rumped Marshbird <i>Pseudoleistes guirahuro</i>	–	–	1	–	–	–	11-20	11-20	6.0	5.7	2–10	2	Cu
White-browed Blackbird <i>Sturnella supercilialis</i>	–	–	–	–	–	–	–	–	4.5	0.7	4–5	2	Gr
Shiny / Screaming Cowbird <i>Molothrus bonariensis</i> / <i>rufoaxillaris</i>	–	–	9	1	–	–	11-3	12-31	1.2	0.4	1–2	11	Bp

<sup>a</sup>Letters denote the months of September–February<sup>b</sup>Month-day<sup>c</sup>Bp = brood parasite; Ca = cavity; Cu = cup; En = enclosed; Gr = ground (see Methods for definitions)

Sapucái, 226 likely represent breeding residents, five are non-breeding Neotropical austral migrants, and two are non-breeding Nearctic migrants (Appendix 1; definitions based on Hayes 1995b). Thus, the egg collections from Sapucái represent only 29.2% of the species presumed to breed there, but more realistically only a quarter of the breeding avifauna because additional species undoubtedly occurred there and probably nested as well (e.g., see Hayes & Scharf [1995] for other species recorded nearby at Parque Nacional Ybycuí).

The two species with the largest clutch sizes, the Smooth-billed Ani (*Crotophaga ani*) and Guira Cuckoo (*Guira guira*), are known to nest communally (e.g., Davis 1940a, b); thus, the

eggs of each “clutch” were likely laid by more than one female.

In the USNM collection, unidentified eggs from the cowbird genus *Molothrus* were recorded in 10 of 19 clutches of the Fork-tailed Flycatcher (*Tyrannus savana*). The brood parasite was almost certainly the Shiny Cowbird (*M. bonariensis*), because the sympatric Screaming Cowbird (*M. rufoaxillaris*) is a brood parasite specialist known to parasitize only three species of icterids (Fraga 1996, Mermoz & Rebores 1996).

**BREEDING SEASON:** All eggs were collected between the months of September and February (Table 1). Roughly two-thirds of the species were recorded breeding during October and



November, which represent the peak of the breeding season; very few species of birds were recorded incubating in September and February, at the extremes of the breeding season (Table 1).

**SAMPLING BIAS:** Of the 226 species presumed to breed at Sapucái, the egg collection is represented by 22 (30.1%) of the nonpasserine species ( $n = 73$  species), 20 (22.0%) of the suboscine passerines ( $n = 91$  species), and 21 (33.9%) of the oscine passerines ( $n = 62$  species; see Appendix 1). The proportion of species from all three groups are equally represented in the collection ( $\chi^2 = 2.87$ ,  $df = 2$ ,  $P = 0.24$ ).

The number of clutches collected per species varied significantly among birds belonging to the three taxonomic groups (Table 3), with significantly more clutches per species for oscine passerines than for suboscine passerines; no

other pairwise comparisons were significant. The number of clutches per species varied significantly among birds constructing different types of nests (Table 3), with significantly more clutches collected for cup-nesting species than for cavity-nesting species; no other pairwise comparisons were significant. The number of clutches per species did not differ significantly between migrant and non-migrant species (Table 3) or among birds belonging to different body size categories ( $r_s = 0.11$ ,  $n = 63$ ,  $P > 0.30$ ).

There was a significant correlation between the number of clutches per species and the three measures for the timing of reproduction: early egg date ( $r_s = -0.51$ ,  $n = 61$  species,  $P < 0.001$ ), late egg date ( $r_s = 0.78$ ,  $n = 61$ ,  $P < 0.001$ ), and duration of incubation ( $r_s = 0.90$ ,  $n = 61$ ,  $P < 0.001$ ). When the analysis was restricted to spe-

Table 2. Number of bird species incubating per month based on range of dates of nests with eggs.

Variable	Month						<i>n</i>
	S	O	N	D	J	F	
All species	2	41	44	29	14	4	63
Taxonomic group <sup>a</sup>							
Non-passerines	0	16	12	10	5	1	22
Suboscine passerines	0	12	12	7	3	0	20
Oscine passerines	2	13	20	12	6	3	21
Type of nest <sup>b</sup>							
Ground nest	0	8	9	5	2	0	13
Cup nest	1	15	23	16	10	3	26
Enclosed nest	0	8	4	2	1	0	9
Cavity nest	1	9	8	4	1	1	14
Annual movements <sup>c</sup>							
Migrant	0	1	6	1	0	0	6
Non-migrant	2	40	38	28	14	4	57

<sup>a</sup> $\chi^2 = 7.44$ ,  $df = 10$ ,  $P = 0.68$

<sup>b</sup> $\chi^2 = 11.49$ ,  $df = 15$ ,  $P = 0.72$

<sup>c</sup> $\chi^2 = 7.12$ ,  $df = 5$ ,  $P = 0.21$

Table 3. Number of clutches per species for birds belonging to different taxonomic groups, constructing different nest types, and exhibiting variation in annual movements.

Variable	Number of clutches / species			
	$\bar{X}$	SD	<i>n</i>	Range
Taxonomic group <sup>a</sup>				
Non-passerines	5.86	4.65	22	1–15
Suboscine passerines	5.30	8.53	20	1–36
Oscine passerines	10.43	9.81	21	1–35
Type of nest <sup>b</sup>				
Ground nest	4.77	2.86	13	1–11
Cup nest	10.73	9.17	26	1–36
Enclosed nest	3.44	5.25	9	1–17
Cavity nest	5.07	9.06	14	1–35
Annual movements <sup>c</sup>				
Migrant	7.33	14.09	6	1–36
Non-migrant	7.19	7.44	57	1–35

<sup>a</sup> $H = 6.41$ ,  $P = 0.04$ <sup>b</sup> $H = 12.47$ ,  $P = 0.01$ <sup>c</sup> $z = 0.04$ ,  $P = 0.97$ 

cies with data for six or more clutches, sample size was no longer correlated with the timing of reproduction: early egg date ( $r_s = -0.24$ ,  $n = 24$ ,  $P > 0.20$ ), late egg date ( $r_s = 0.28$ ,  $n = 24$ ,  $P > 0.10$ ), and duration of incubation ( $r_s = 0.32$ ,  $n = 24$ ,  $P > 0.05$ ). Subsequent analyses of the variables potentially affecting the timing of reproduction were restricted to the 24 species with data for six or more clutches.

There was no significant correlation between the number of clutches per species and clutch size ( $r_s = -0.09$ ,  $n = 60$ ,  $P > 0.45$ ). Subsequent analyses of the variables potentially affecting clutch size included 60 species with data for one or more clutches.

**TAXONOMIC GROUP:** The number of species breeding per month did not vary significantly among the three taxonomic groups (Table 2). There was no significant variation among spe-

cies belonging to the three taxonomic groups for any reproductive measure (Table 4).

**TYPE OF NEST:** The number of species breeding per month did not vary among species constructing different types of nests (Table 2). There was no significant variation among species constructing different nest types for any reproductive measure (Table 5).

**BODY SIZE:** Among all species of birds combined, body size was not significantly correlated with early egg date ( $r_s = -0.02$ ,  $n = 24$ ,  $P > 0.90$ ), late egg date ( $r_s = -0.25$ ,  $n = 24$ ,  $P > 0.10$ ), duration of incubation ( $r_s = 0.08$ ,  $n = 24$ ,  $P > 0.50$ ), or clutch size ( $r_s = 0.19$ ,  $n = 60$ ,  $P > 0.10$ ).

Body size varied significantly among birds belonging to the three taxonomic groups ( $H = 21.11$ ,  $P < 0.001$ ) and constructing four types of nests ( $H = 10.42$ ,  $P = 0.02$ ). Within each taxonomic group, the only reproductive measure sig-

nificantly correlated with body size was clutch size for non-passerines (Table 6). Within each nest type group, no reproductive measure was significantly correlated with body size (Table 6).

**ANNUAL MOVEMENTS:** Of the 63 species of birds represented by the Sapucáí egg collections, only six are known to be long-distance Neotropical austral migrants (sensu Hayes 1995b): Piratic Flycatcher (*Legatus leucophaeus*), Streaked Flycatcher (*Myiodynastes maculatus*), Tropical Kingbird (*Tyrannus melancholicus*), Fork-tailed Flycatcher (*Tyrannus savanna*), Red-eyed Vireo (*Vireo olivaceus*), and Gray-breasted Martin (*Progne chalybea*). The number of species breeding per month did not vary between mi-

grant and non-migrant species (Table 2). Clutch size did not vary significantly between migrant ( $\bar{X} = 2.77$ ,  $SD = 0.77$ ,  $n = 6$ , range = 2.0–4.0) and non-migrant species ( $\bar{X} = 2.84$ ,  $SD = 0.94$ ,  $n = 54$ , range = 1.0–6.0;  $z = 0.04$ ,  $P = 0.97$ ). Sample sizes were too low to permit comparisons of reproductive timing between migrant and non-migrant species.

## DISCUSSION

**FAUNAL COMPOSITION:** The egg collection from Sapucáí represents one of the largest from a single locality in South America. Nevertheless, the collection represents only a fraction (28.5%) of the species collected from the locality and presu-

Table 4. Comparisons of early egg date, late egg date, duration of incubation and clutch size among taxonomic groups. For measures of reproductive timing, only species with six or more clutches are included.

Variable/taxonomic group	$\bar{X}$	SD	$n$	Range
Early egg date <sup>a</sup>				
Non-passerines	10.63	0.57	9	10.00–11.53
Suboscine passerines	10.56	0.45	4	10.29–11.23
Oscine passerines	10.24	0.41	11	9.73–11.07
Late egg date <sup>b</sup>				
Non-passerines	12.97	0.69	9	11.93–14.43
Suboscine passerines	12.69	0.44	4	12.10–13.03
Oscine passerines	13.21	0.70	11	12.16–14.21
Duration of incubation <sup>c</sup>				
Non-passerines	2.33	0.90	9	1.11–4.14
Suboscine passerines	2.13	0.48	4	1.71–2.71
Oscine passerines	2.97	0.98	11	1.19–4.48
Clutch size <sup>d</sup>				
Non-passerines	2.67	1.00	20	1.0–5.2
Suboscine passerines	2.72	0.75	20	1.6–5.0
Oscine passerines	3.11	0.97	20	2.0–6.0

<sup>a</sup> $H = 5.34$ ,  $P = 0.07$

<sup>b</sup> $H = 1.86$ ,  $P = 0.41$

<sup>c</sup> $H = 4.07$ ,  $P = 0.13$

<sup>d</sup> $H = 3.21$ ,  $P = 0.20$

Table 5. Comparisons of early egg date, late egg date, duration of incubation, and clutch size among birds constructing different nest types. For measures of reproductive timing, only species with six or more clutches are included, and enclosed and cavity nests are combined (a brood parasitic species is excluded).

Variable/nest type	$\bar{X}$	SD	<i>n</i>	Range
Early egg date <sup>a</sup>				
Ground nest	10.53	0.70	4	10.00–11.53
Cup nest	10.41	0.47	15	9.93–11.23
Enclosed/cavity nest	10.33	0.50	4	9.73–10.97
Late egg date <sup>b</sup>				
Ground nest	12.89	0.31	4	12.52–13.19
Cup nest	13.10	0.72	15	11.93–14.43
Enclosed/cavity nest	13.01	0.88	4	12.16–14.21
Duration of incubation <sup>c</sup>				
Ground nest	2.31	0.81	4	1.11–2.90
Cup nest	2.69	0.89	15	1.44–4.25
Enclosed/cavity nest	2.68	1.36	4	1.19–4.48
Clutch size <sup>d</sup>				
Ground nest	2.84	1.07	13	1.7–5.2
Cup nest	2.75	0.91	24	1.6–6.0
Enclosed nest	3.03	0.89	9	2.0–5.0
Cavity nest	2.83	0.88	14	1.0–4.0

<sup>a</sup> $H = 0.06$ ,  $P = 0.97$

<sup>b</sup> $H = 0.49$ ,  $P = 0.78$

<sup>c</sup> $H = 0.10$ ,  $P = 0.95$

<sup>d</sup> $H = 1.37$ ,  $P = 0.71$

med to breed, thus demonstrating the incomplete nature of the data. Furthermore, the number of clutches collected per species was biased toward oscine passerines, particularly those species with cup shaped nests. The number of clutches from suboscine passerines and cavity nesting species were underrepresented in the collection.

**BREEDING SEASON:** The seasonal distribution of incubating birds at Sapucái and farther west at Estancia Ytañú, Departamento Central (Dalglish 1889), indicates that the breeding season in subtropical Paraguay begins with the austral spring and extends into summer. This strongly seasonal pattern is more typical of avian com-

munities in subtropical or temperate regions (e.g., Mason 1985, de la Peña 1995, 2010, Mallet-Rodrigues 2005, Auer et al. 2007) and in relatively dry tropical regions (e.g., Poulin et al. 1992, Hayes & Samad 2002, Marini et al. 2012) than in more humid tropical regions of South America (e.g., Marchant 1959, Snow & Snow 1964, Cruz & Andrews 1989, Johnson et al. 2012, Stouffer et al. 2013). Some clutches recorded later during the year may represent a second or third clutch during the same breeding season. For example, Smith & Betuel (2006) provided evidence of multiple clutches in the Picui Ground-Dove (*Columbina picui*) nesting

in southern Paraguay. Unfortunately little information is available on the frequency of multiple clutches of birds in Paraguay.

The timing of reproduction by incubating birds at Sapucái does not appear to be related to taxonomic group, type of nest constructed, body size, or annual movements. However, a few non-passerines, including the Eared Dove (*Zenaidura macroura*) and the Picui Ground-Dove (*Columbina picui*), apparently incubate during every month of the year in Santa Fe, Argentina, whereas the Southern Caracara (*Caracara plancus*) begins incubating as early as June (de la Peña 1995, 2010). A similar pattern may occur in Paraguay as well (Smith & Beuel 2006). A much larger sample size of nesting birds from Sapucái might have revealed significant patterns in the timing of reproduction. At El Rey National Park in Salta, Argentina, species with enclosed nests initiated breeding significantly earlier than species with open nests (Auer et al. 2007). A similar but non-significant pattern occurred at Sapucái.

**CLUTCH SIZE:** Yom-Tov et al. (1994) found significant differences in clutch size among families of Passerine birds in southern South America, and also found that oscines averaged significantly larger clutch sizes than suboscines. A similar but non-significant pattern emerged from Sapucái, where mean clutch size for suboscines (2.72) was almost identical to the data from Yom-Tov et al. (1994; 2.73) but considerably lower for the oscines (3.11 at Sapucái, 3.32 in South America). Even with an a posteriori Mann-Whitney *U* test comparing the two groups at Sapucái, there was no significant difference in clutch size ( $z = 1.16$ ,  $P = 0.24$ ).

The type of nest constructed by birds is thought to be a factor affecting clutch size in birds, with clutch sizes being larger in relatively secure nests than in more vulnerable nests (e.g., Lack 1968, Klomp 1970), but the interpretations of the data are controversial and other factors such as the size, shape, and structure of the nest may be more important (e.g., Snow 1978). Yom-Tov et al. (1994) found no significant differences

**Table 6.** Spearman rank correlation coefficients ( $r_s$ ) of body size with early egg date, late egg date, duration of incubation, and clutch size for birds belonging to different taxonomic groups and nest types. Sample sizes were too small for some variables.

Variable	Early egg date		Late egg date		Duration of incub.		Clutch size	
	$r_s$	$n$	$r_s$	$n$	$r_s$	$n$	$r_s$	$n$
Taxonomic group								
Non-passerines	-0.11	9	-0.32	9	-0.15	9	0.48 <sup>a</sup>	20
Suboscine passerines	—	—	—	—	—	—	0.37	20
Oscine passerines	-0.13	11	-0.49	11	-0.39	11	0.29	20
Type of nest								
Ground nest	—	—	—	—	—	—	0.44	13
Cup nest	-0.18	15	-0.23	15	-0.24	15	0.29	24
Enclosed nest	—	—	—	—	—	—	0.31	9
Cavity nest	—	—	—	—	—	—	0.10	14

<sup>a</sup> $P < 0.05$

in clutch size among birds constructing four types of nests (cup, hole, enclosed nest, and enclosed mud nest) in southern South America. However, Auer et al. (2007) found that clutch size was greater for species with cavity nests than for species with enclosed or cup nests. The data from Sapucáí failed to demonstrate differences among birds constructing different types of nests. A potential problem with such comparisons across a diversity of taxa is the effect of phylogenetic constraints on the evolution of clutch size (e.g., Klomp 1970, Yom-Tov et al. 1994).

The effects of body size on clutch size and its significance are poorly understood. A negative correlation between body size and clutch size was reported for European passerines (Saether 1985) and for North American and European landbirds (Böhning-Gaese et al. 2000). However, no correlation was found among New World passerines (Kulesza 1990) and southern South American passerines (Yom-Tov et al. 1994). The data from Sapucáí revealed a significantly positive correlation between body size and clutch size for non-passerines, but not for any other taxonomic group or among species constructing different types of nests. Body size varied more among non-passerines (e.g., ranging from small hummingbirds to large tinamous at Sapucáí;  $\bar{X}$  body size class = 5.91, SD = 2.09, range = 1-10,  $n = 22$ ) than among passerines ( $\bar{X} = 3.22$ , SD = 1.22, range = 2-7,  $n = 41$ ; Bartlett's test for equality of variances,  $F = 2.96$ ,  $P = 0.002$ ); thus, a significant correlation between body size and clutch size among non-passerines should be less surprising.

Böhning-Gaese et al. (2000) reported that migrant species of landbirds in North America and Europe had smaller clutch sizes than non-migratory species. Yom-Tov et al. (1994) predicted that migratory species in southern South America would have a larger clutch size than non-migratory species, but were unable to find a significant difference. The data from Sapucáí failed to find a significant difference in clutch

size between migrant and non-migrant species.

The clutch size data used by Yom-Tov et al. (1994) was based primarily upon general statements in the literature rather than actual data. Comparisons of geographical variation in clutch size should be more accurate if based upon actual data from different localities, such as the data presented herein from Sapucáí. Much more data are needed from a variety of localities to accurately test hypotheses regarding the adaptive significance of the timing of reproduction and variation in clutch size among South American birds.

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## APPENDIX 1

Species of birds collected at Sapucaí, Departamento Paraguari, Paraguay (see Methods for sources). The taxonomy follows Remsen et al. (2014). Status codes: B = breeding confirmed; B? = breeding suspected; NA = non-breeding Nearctic migrant; NT = non-breeding Neotropical migrant.

## NON-PASSERINES

TINAMIDAE: Solitary Tinamou (*Tinamus solitarius*), B; Undulated Tinamou (*Crypturellus undulatus*), B?; Small-billed Tinamou (*Crypturellus parvirostris*), B; Tataupa Tinamou (*Crypturellus tataupa*), B; Red-winged Tinamou (*Rhynchotus rufescens*), B; Spotted Nothura (*Nothura maculosa*), B; ACCIPITRIDAE: Ornate Hawk-Eagle (*Spizaetus ornatus*), B?; Plumbeous Kite (*Ictinia plumbea*), B?; Bicolored Hawk (*Accipiter bicolor*), B; Savanna Hawk (*Buteogallus meridionalis*), B?; Great Black Hawk (*Buteogallus urubitinga*), B?; Roadside Hawk (*Rupornis magnirostris*), B?; Harris's Hawk (*Parabuteo unicinctus*), B?; RALLIDAE: Gray-necked Wood-Rail (*Aramides cajaneus*), B?; Blackish Rail (*Pardirallus nigricans*), B?; Plumbeous Rail (*Pardirallus sanguinolentus*), B?; Purple Gallinule (*Porphyrio martinicus*), B?; CHARADRIIDAE: Southern Lapwing (*Vanellus chilensis*), B; RECURVIROSTRIDAE: Black-necked Stilt (*Himantopus mexicanus*), B?; SCOLOPACIDAE: South American Snipe (*Gallinago paraguaiiae*), B; Solitary Sandpiper (*Tringa solitaria*), NA; JACANIDAE: Wattled Jacana (*Jacana jacana*), B?; LARIDAE: Brown-hooded Gull (*Chroicocephalus maculipennis*), NT; COLUMBIDAE: Pale-vented Pigeon (*Patagioenas cayennensis*), B; Eared Dove (*Zenaida auriculata*), B?; White-tipped Dove (*Leptotila verreauxi*), B; Violaceous Quail-Dove (*Geotrygon violacea*), B?; Ruddy Ground Dove (*Columbina talpacoti*), B; Picui Ground Dove (*Columbina picui*), B?; CUCULIDAE: Squirrel Cuckoo (*Piaya cayana*), B?; Dark-billed Cuckoo (*Coccyzus melacoryphus*), B?; Yellow-billed Cuckoo (*Coccyzus americanus*), NA; Greater Ani (*Crotophaga major*), B?; Smooth-billed Ani (*Crotophaga ani*), B; Guira Cuckoo (*Guira guira*), B; Striped Cuckoo (*Tapera naevia*), B?; Pheasant Cuckoo (*Dromococcyx phasianellus*), B?; TYTONIDAE: Barn Owl (*Tyto alba*), B?; STRIGIDAE: Tropical Screech-Owl (*Megascops choliba*), B; Ferruginous Pygmy-Owl (*Glucidium brasilianum*), B?; Burrowing Owl (*Athene cunicularia*), B?; Buff-fronted Owl (*Aegolius harrisii*), B?; CAPRIMULGIDAE: Nacunda Nighthawk (*Chordeiles nacunda*), B; Common Pauraque (*Nyctidromus albicollis*), B; Little Nightjar (*Setopagis parvula*), B; APODIDAE: Vaux's Swift (*Chaetura vauxi*), B?; TROCHILIDAE: Glittering-bellied Emerald (*Chlorostilbon lucidus*), B?; Fork-tailed Woodnymph (*Thalurania furcata*), B?; Gilded Sapphire (*Hylocharis chrysura*), B; ALCEDINIDAE: Green Kingfisher (*Chloroceryle americana*), B?; MOMOTIDAE: Rufous-capped Motmot (*Baryphthengus ruficapillus*), B?; BUCCONIDAE: White-eared Puffbird (*Nystalus chacuru*), B?; Rusty-breasted Nunlet (*Nonnulla rubecula*), B?; RAMPHASTIDAE: Red-breasted Toucan (*Ramphastos dicolorus*), B?; Chestnut-eared Aracari (*Pteroglossus castanotis*), B?; PICIDAE: White-barred Piculet (*Picumnus cirratus*), B; White Woodpecker (*Melanerpes candidus*), B?; Yellow-fronted Woodpecker (*Melanerpes flavifrons*), B; White-spotted Woodpecker (*Veniliornis spilogaster*), B?; Little Woodpecker (*Veniliornis passerinus*), B?; White-browed Woodpecker (*Piculus aurulentus*), B?; Green-barred Woodpecker (*Colaptes melanochloros*), B; Campo Flicker (*Colaptes campestris*), B; Pale-crested Woodpecker (*Celeus lugubris*), B?; Helmeted Woodpecker (*Dryocopus galeatus*), B?; Lineated Woodpecker (*Dryocopus lineatus*), B; Robust Woodpecker (*Campephilus robustus*), B?; FALCONIDAE: Barred Forest-Falcon (*Micrastur ruficollis*), B?; Southern Caracara (*Caracara plancus*), B?; Chimango Caracara (*Milvago chimango*), B?; American Kestrel (*Falco sparverius*), B; Bat Falcon (*Falco rufigularis*), B?; PSITTACIDAE: Red-capped Parrot (*Pionopsitta pileata*), B?; Blue-winged Parrotlet (*Forpus xanthopterygius*), B?; Reddish-bellied Parakeet (*Pyrrhura frontalis*), B?; White-eyed Parakeet (*Psittacara leucophthalmus*), B?.

## SUBOSCINE PASSERINES

THAMNOPHILIDAE: Spot-backed Antshrike (*Hypodaleus guttatus*), B?; Barred Antshrike (*Thamnophilus doliatus*), B?; Variable Antshrike (*Thamnophilus caerulescens*), B?; Plain Antvireo (*Dysithamnus mentalis*), B?; Rufous-winged Antwren (*Herpsilochmus rufimarginatus*), B?; Dusky-tailed Antbird (*Drymophila malura*), B?; CONOPOPHAGIDAE: Rufous Gnateater (*Conopophaga lineata*), B?; FORMICARIIDAE:



Short-tailed Antthrush (*Chamaeza campanisona*), B?; FURNARIIDAE: Rufous-breasted Leaf-tosser (*Sclerurus scansor*), B; Olivaceous Woodcreeper (*Sittasomus griseicapillus*), B?; Planalto Woodcreeper (*Dendrocolaptes platyrostris*), B?; White-throated Woodcreeper (*Xiphocolaptes albicollis*), B?; Lesser Woodcreeper (*Xiphorhynchus fuscus*), B?; Great Rufous Woodcreeper (*Xiphocolaptes major*), B; Narrow-billed Woodcreeper (*Lepidocolaptes angustirostris*), B?; Streaked Xenops (*Xenops rutilans*), B?; Rufous Hornero (*Furnarius rufus*), B; Sharp-tailed Streamcreeper (*Lochmias nematura*), B?; Black-capped Foliage-gleaner (*Philydor atricapillus*), B?; Buff-fronted Foliage-gleaner (*Philydor rufum*), B?; Ochre-breasted Foliage-gleaner (*Anabacerthia lichtensteini*), B?; Buff-browed Foliage-gleaner (*Syndactyla rufosuperciliata*), B?; White-eyed Foliage-gleaner (*Automolus leucophthalmus*), B?; Greater Thornbird (*Phacellodomus ruber*), B?; Firewood-Gatherer (*Anumbius anumbi*), B; Chotoy Spinetail (*Schoeniophylax phryganophila*), B; Yellow-throated Spinetail (*Certhiaxis cinnamomea*), B?; Rufous-capped Spinetail (*Synallaxis ruficapilla*), B?; Chicli Spinetail (*Synallaxis spixi*), B?; Pale-breasted Spinetail (*Synallaxis albescens*), B?; Sooty-fronted Spinetail (*Synallaxis frontalis*), B?; Gray-bellied Spinetail (*Synallaxis cinerascens*), B?; TYRANNIDAE: Rough-legged Tyrannulet (*Phyllomyias burmeisteri*), B?; Greenish Tyrannulet (*Phyllomyias virescens*), B?; Gray Elaenia (*Myiopagis caniceps*), B?; Greenish Elaenia (*Myiopagis viridicata*), B?; Yellow-bellied Elaenia (*Elaenia flavogaster*), B; Small-billed Elaenia (*Elaenia parvirostris*), B?; Olivaceous Elaenia (*Elaenia mesoleuca*), B?; Suiriri Flycatcher (*Suiriri suiriri*), B?; White-crested Tyrannulet (*Serpophaga subcristata*), B?; Mouse-colored Tyrannulet (*Phaeomyias murina*), B?; Yellow Tyrannulet (*Capsiempis flaveola*), B?; Bearded Tachuri (*Polystictus pectoralis*), B?; Southern Antpipit (*Corythopsis delalandi*), B?; Southern Bristle-Tyrant (*Phylloscartes eximius*), B?; Mottle-cheeked Tyrannulet (*Phylloscartes ventralis*), B?; Gray-hooded Flycatcher (*Mionectes rufiventris*), B?; Sepia-capped Flycatcher (*Leptopogon amaurocephalus*), B; Sharp-tailed Tyrant (*Culicivora caudacuta*), B?; Eared Pygmy-Tyrant (*Myiornis auricularis*), B?; Pearly-vented Tody-Tyrant (*Hemitriccus margaritaceiventer*), B?; Ochre-faced Tody-Flycatcher (*Todirostrum plumbeiceps*), B?; Yellow-olive Flycatcher (*Tolmomyias sulphurescens*), B; White-throated Spadebill (*Platyrinchus mystaceus*), B?; Russet-winged Spadebill (*Platyrinchus leucoryphus*), B?; Euler's Flycatcher (*Lathrotriccus eulerei*), B?; Fuscous Flycatcher (*Cnemotriccus fuscatus*), B?; Tropical Pewee (*Contopus cinereus*), B?; Vermilion Flycatcher (*Pyrocephalus rubinus*), B?; Cinereous Tyrant (*Knipolegus striaticeps*), B?; Blue-billed Black-Tyrant (*Knipolegus cyanirostris*), NT; Spectacled Tyrant (*Hymenops perspicillatus*), B?; Yellow-browed Tyrant (*Satrapa icterophrys*), B?; Gray Monjita (*Xolmis cinereus*), B; White Monjita (*Xolmis irupero*), B?; Streamer-tailed Tyrant (*Gubernetes yetapa*), B; Strange-tailed Tyrant (*Alectrurus risora*), B?; Long-tailed Tyrant (*Colonia colonus*), B?; Cattle Tyrant (*Machetornis rixosa*), B; Piratic Flycatcher (*Legatus leucophaeus*), B; Great Kiskadee (*Pitangus sulphuratus*), B; Three-striped Flycatcher (*Conopias trivirgata*), B?; Streaked Flycatcher (*Myiodynastes maculatus*), B; Boat-billed Flycatcher (*Megarynchus pitangua*), B; Tropical Kingbird (*Tyrannus melancholicus*), B; Fork-tailed Flycatcher (*Tyrannus savana*), B; Sirystes (*Sirystes sibilator*), B?; Rufous Casiornis (*Casiornis rufus*), B?; Short-crested Flycatcher (*Myiarchus ferox*), B; Brown-crested Flycatcher (*Myiarchus tyrannulus*), B; OXYRUNCIDAE Sharpbill (*Oxyruncus cristatus*), B?; PIPRIDAE: Swallow-tailed Manakin (*Chiroxiphia caudata*), B; Band-tailed Manakin (*Pipra fasciicauda*), B?; TITYRIDAE: Black-crowned Tityra (*Tityra inquisitor*), B?; Black-tailed Tityra (*Tityra cayana*), B?; Greenish Schiffornis (*Schiffornis virescens*), B?; Green-backed Becard (*Pachyramphus viridis*), B; Chestnut-crowned Becard (*Pachyramphus castaneus*), B?; White-winged Becard (*Pachyramphus polychopterus*), B?; Crested Becard (*Pachyramphus validus*), B?; INCERTAE CEDIS: Wing-barred Manakin (*Piprites chloris*), B?.

#### OSCINE PASSERINES

VIREONIDAE: Rufous-browed Peppershrike (*Cyclarhis gujanensis*), B?; Red-eyed Vireo (*Vireo olivaceus*), B; Rufous-crowned Greenlet (*Hylophilus poicilotis*), B?; CORVIDAE: Purplish Jay (*Cyanocorax cyano-melas*), B; Plush-crested Jay (*Cyanocorax chrysops*), B; HIRUNDINIDAE: Gray-breasted Martin (*Progne chalybea*), B; White-rumped Swallow (*Tachycineta leucorrhoa*), B?; TROGLODYTIDAE: House Wren (*Troglodytes aedon*), B; POLIOPTILIDAE: Cream-bellied Gnatcatcher (*Polioptila lactea*), B?; TURDIDAE: Pale-breasted Thrush (*Turdus leucomelas*), B; Rufous-bellied Thrush (*Turdus rufiventris*), B; Creamy-bellied



Thrush (*Turdus amaurochalinus*), B; White-necked Thrush (*Turdus albicollis*), B?; MIMIDAE: White-banded Mockingbird (*Mimus triurus*), NT; MOTACILLIDAE: Yellowish Pipit (*Anthus lutescens*), B?; THRAUPIDAE: Red-crested Cardinal (*Paroaria coronata*), B?; Magpie Tanager (*Cissopis leveriana*), B?; Hooded Tanager (*Nemosia pileata*), B?; Chestnut-headed Tanager (*Pyrrhocomma ruficeps*), B?; Black-goggled Tanager (*Trichothraupis melanops*), B?; Ruby-crowned Tanager (*Tachyphonus coronatus*), B?; Fawn-breasted Tanager (*Pipraeidea melanonota*), B?; Sayaca Tanager (*Thraupis sayaca*), B; Chestnut-backed Tanager (*Tangara preciosa*), B?; Burnished-buff Tanager (*Tangara cayana*), B?; Swallow-Tanager (*Tersina viridis*), B?; Blue Dacnis (*Dacnis cayana*), B?; Guira Tanager (*Hemithraupis guira*), B?; Chestnut-vented Conebill (*Conirostrum speciosum*), B?; Uniform Finch (*Haplospiza unicolor*), B?; Long-tailed Reed-Finch (*Donacospiza albifrons*), B?; Black-and-rufous Warbling-Finch (*Poospiza nigrorufa*), NT; Saffron Finch (*Sicalis flaveola*), B?; Wedge-tailed Grass-Finch (*Emberizoides herbicola*), B; Great Pampa-Finch (*Embernagra platensis*), B; Rusty-collared Seedeater (*Sporophila collaris*), B?; Double-collared Seedeater (*Sporophila caerulea*), B?; Pearly-breasted Seedeater (*Sporophila pileata*), B?; Tawny-bellied Seedeater (*Sporophila hypoxantha*), B?; Dark-throated Seedeater (*Sporophila ruficollis*), B?; Red-crested Finch (*Coryphospingus cucullatus*), B; EMBERIZIDAE: Rufous-collared Sparrow (*Zonotrichia capensis*), B; Grassland Sparrow (*Ammodramus humeralis*), B; Saffron-billed Sparrow (*Arremon flavirostris*), B?; CARDINALIDAE: Red-crowned Ant-Tanager (*Habia rubica*), B?; Indigo Grosbeak (*Cyanoloxia glaucoacaerulea*), NT; Ultramarine Grosbeak (*Cyanocompsa brissonii*), B?; PARULIDAE: Masked Yellowthroat (*Geothlypis aequinoctialis*), B; Tropical Parula (*Setophaga pitiauyumi*), B?; White-browed Warbler (*Myiothlypis leucoblephara*), B?; Golden-crowned Warbler (*Basileuterus culicivorus*), B; ICTERIDAE: Variable Oriole (*Icterus pyrrhopterus*), B; Chopi Blackbird (*Gnorimopsar chopi*), B; Unicolored Blackbird (*Agelasticus cyanopus*), B?; Chestnut-capped Blackbird (*Chrysomus ruficapillus*), B?; Yellow-rumped Marshbird (*Pseudoleistes guirahuro*), B; Screaming Cowbird (*Molothrus rufoaxillaris*), B?; Shiny Cowbird (*Molothrus bonariensis*), B; White-browed Blackbird (*Sturnella superciliaris*), B; FRINGILLIDAE: Hooded Siskin (*Sporagra magellanica*), B?; Purple-throated Euphonia (*Euphonia chlorotica*), B?; Violaceous Euphonia (*Euphonia violacea*), B?; Golden-rumped Euphonia (*Euphonia cyanocephala*), B?; Chestnut-bellied Euphonia (*Euphonia pectoralis*), B?; Blue-naped Chlorophonia (*Chlorophonia cyanea*), B?.