

COLOR PLATE. Chapada Flycatcher, a new species of tyrant-flycatcher (Tyrannidae: Suiriri) from the cerrado region of central South America. The male is pictured in profile on the left; the female is displaying with wings raised, on the right. From a watercolor painting by Daniel F. Lane.

A CRYPTIC NEW SPECIES OF FLYCATCHER (TYRANNIDAE: *SUIRIRI*) FROM THE CERRADO REGION OF CENTRAL SOUTH AMERICA

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ABSTRACT.—A new species of tyrant flycatcher (*Suiriri islerorum*) is described from the cerrado region of Brazil and adjacent eastern Bolivia. The species previously had been confused with *Suiriri suiriri affinis*, with which it is syntopic at multiple sites. The new species was first identified by voice. Although cryptically similar to *S. s. affinis* in many respects, the new species is readily identified by all vocalizations, bill size, color pattern of the tail, and shape of the central rectrices. Most distinctive are the male–female duets, which are accompanied by dramatic wing-lifting displays not performed by any congeners. Reciprocal playback experiments of tape-recorded vocalizations. We provide information on the natural history of the new flycatcher, along with spectrograms of its various vocalizations. We also provide vocal analysis of all other named taxa in *Suiriri*, and discuss the various intrageneric relationships. In particular, *S. s. affinis* and *S. s. bahiae*, although distinct morphologically, are vocally and behaviorally similar, and respond to one another's vocalizations in playback experiments. *Received 27 December 1999, accepted 5 September 2000*.

THE GENUS SUIRIRI has been the focus of taxonomic debate for decades. Two species traditionally were recognized, a short-billed, whitebellied nominate form Suiriri suiriri; and a longer-billed, yellow-bellied form, S. affinis. The apparent intermediacy of a large series of Suiriri from northeastern Paraguay led Zimmer (1955) to suggest that the two taxa were conspecific. Meyer de Schauensee (1966) and Traylor (1979) followed Zimmer in recognizing only one species of Suiriri, whereas Short (1975) did not agree that Paraguayan birds showed signs of intergradation and continued to recognize two species. Traylor (1982) reexamined the Paraguayan material in the American Museum of Natural History (AMNH), and found it as described by Zimmer, concurring that S. suiriri and S. affinis should be treated as conspecific. More recent authors have remained divided: Sibley and Monroe (1990) recognized two species of Suiriri, whereas Ridgely and Tudor (1994) recognized only one. As currently treated, the genus also includes one additional taxon, S. s. bahiae, a yellow-bellied taxon from northeastern Brazil. Hellmayr (1927) treated *bahiae* as a subspecies of *S. affinis*, from which he found it to differ from typical forms by "uppertail coverts dark hair brown like the tail; rectrices without any yellowish at the base and without the pale brownish apical band."

Zimmer (1955) pointed out an additional complication: five AMNH specimens of S. affinis from Mato Grosso and Goiás, Brazil, all of which were anomalous in having a short, broad-based bill and with the "pale terminal band on the rectrices unusually wide and distinct, exceeding any other specimen at hand whether from the same or other localities and whether suiriri, affinis, or bahiae." Zimmer further noted that "the significance of this combination of characters is completely puzzling, since there is no allied group toward which these features, singly or together, suggest a trend." In his reexamination of Suiriri, Traylor (1982) commented on the five aberrent AMNH specimens and an identical specimen from Maranhão, Brazil (from the Field Museum of Natural History, Chicago; hereafter FMNH). In addition to the short bill and broad, pale tips to the rectrices, the six specimens further could be distinguished from typical affinis by their distinctly broader central rectrices and a lack of

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any contrasting pale edging to those feathers (Traylor 1982). Traylor noted that "ordinarily the close correlation of two such discrete and unrelated characters as the short bill and the coloration and shape of the rectrices would be strong evidence that we have two sibling species. I think that eventually this will prove to be true, but the possibility that the short-billed birds may somehow be related to the intergradation between *affinis* and *suiriri* cannot be ignored at this time." He concluded by stating "most important, without field studies of the various taxa, it is useless to speculate."

During the course of several years of field work at various sites in Brazil, Zimmer and Whittaker found that there were two markedly different vocal types of yellow-bellied Suiriri, one of which was relatively widespread, occurring from Amapá to Bahia to Goiás; and the other which we knew only from the Chapada dos Guimarães region of Mato Grosso. The first type included birds that, by both distribution and morphological characters, clearly were assignable to S. s. bahiae, as well as birds that appeared to be typical of S. s. affinis. The second type was distinctive not only for its vocalizations, but also for its dramatic wing-flapping displays that invariably accompanied all territorial duets by mated pairs (see below). Reciprocal playback experiments conducted at multiple sites revealed that the two vocal types did not respond to one anothers' vocalizations. In September 1998, we found the two vocal types occurring syntopically near Cuiabá, Mato Grosso, Brazil. Close comparison revealed that one vocal type was noticeably short-billed compared to the other and had a distinct buffy terminal fringe to the tail, and that the birds were always assortatively paired with their own vocal and morphological types.

Suspecting that the short-billed birds represented the same birds as the anomalous specimens reported by Zimmer and Traylor, we returned to the Cuiabá region in September 1999 with Dionisio Pimentel of the Museu Paraense Emílio Goeldi, Belém (hereafter MPEG) and collected 10 specimens of each vocal type. Prior to collecting, we made voucher tape-recordings of each bird (all recordings to be archived at the Library of Natural Sounds, Cornell Laboratory of Ornithology, Ithaca, New York; hereafter LNS). Tissue samples also were preserved for molecular analysis of genetic differences. All specimens and tissue samples were deposited with the MPEG. We also located additional sites of sympatry between the two vocal types.

METHODS

We made observations of Suiriri at various sites in Mato Grosso, Brazil (August and October 1991, and every September from 1993 to 1999); Pernambuco, Brazil (each January from 1996 to 1999, and February 1996); Goiás, Brazil (January 1996); and Amapá, Brazil (February 1998 and 1999). All measurements used in behavioral data (e.g. distances, heights) are estimates. Sexual identification of birds in the field was based on sex-specific, stereotyped displays or vocalizations, the sexual specificity of which was confirmed by postmortem inspection of specimens that we collected. Mapped distributions (as they appear in this paper) are based entirely on label data from specimens that the senior author examined, on more recent records documented by tape recordings, and on our own collecting sites. Those localities were entered into a sector-based Geographic Information System (Isler 1997) and mapped by Morton Isler.

We assume that vocalizations of *Suiriri*, like those of other suboscines, are mostly or entirely inherited (Kroodsma 1984, 1989; Kroodsma and Konishi 1991), and as such, provide potentially informative characters for systematic study as in other suboscines (Lanyon 1978, Isler et al. 1997, Krabbe and Schulenberg 1997). To analyze vocalizations, we assembled recordings of all named taxa of Suiriri for comparison with our own recordings. Locations and recordists for all recordings examined are listed below. For comparison, vocalizations were categorized as loudsongs, duets, or calls. "Loudsongs" were consistently patterned multinote vocalizations (Isler et al. 1997) given by an individual bird, seemingly in the context of territorial advertisement. Those were given individually by both sexes, but most frequently were incorporated into duets. "Duets" involved simultaneous singing by a pair of Suiriri, and consisted of typical loudsongs of both sexes, combined with other calls. Vocalizations categorized as calls most often were structurally simple (typically involving only one or a few notes; exceptions are noted below) and usually were given in the context of contact vocalizations between mates or family members. Our recordings were made with Sony TCM-5000 tape recorders and Sennheiser ME-80, ME-66, and MKH-70 shotgun microphones. Spectrograms were made by Phyllis Isler on a Macintosh G4 computer using Canary version 1.2.1 (Bioacoustics Research Program, Cornell Laboratory of Ornithology, Ithaca, New York). Canary parameters were standard default except that frame overlap used was \geq 96.88%.

Playback experiments were conducted to determine reactions of *Suiriri* of each type to vocalizations

of the others. In each case, an individual or pair of flycatchers first was presented with a prerecorded tape of another taxon. Each prerecorded tape included a combined 10 to 15 songs and duets (interspersed with calls) from two pairs of birds of a given taxon and geographic locality. For the S. s. suiriri tape, we used only songs and calls because we had no recordings of duets. For all trials, each taxon was represented by a single playback tape consisting of vocalizations of two pairs (or individuals in the case of nominate Suiriri) of birds. During each trial, the tape of 10 to 15 songs and duets was played to conclusion. To avoid confounding effects, a buffer period of about 2 min was used to separate playback of vocalizations of different taxa. Flycatchers that did not respond to playback of other taxa then were presented with a playback tape of their own vocal type. That was done to account for potential seasonal influences by resolving the question of whether birds that were unresponsive in the first trials were discriminating between the different vocalizations, or were generally nonterritorial during the trial period and therefore unresponsive to playback of any kind. Failure to account for seasonal differences in responsiveness has been cited as a potential design weakness in other playback experiments (Kroodsma 1986). Responses to playback were characterized as "strong," "moderate," "weak," or "none." A strong response involved immediate and repeated vocalizations (from previously nonvocalizing birds) as well as approach toward the sound source. A moderate response involved either a cautious approach without vocalizing, or sustained vocalizing without approach. A weak response involved single or unsustained vocalizations (from previously nonvocalizing birds) without approach. The none category includes instances in which birds remained silent (in the case of previously nonvocalizing birds) and did not approach the sound source, as well as instances in which already vocalizing birds neither changed the delivery or rate of their vocalizations, nor approached the sound source. A potential fifth category would be a "negative response," in which the subject bird responded to the sound stimulus by moving farther away. No negative responses to playback were observed from any taxa.

Zimmer examined representative specimens of *Suiriri* (n = 170) for comparison with our 20 specimens from Mato Grosso. Those specimens are housed at the Museu Paraense Emílio Goeldi, Belém, Brazil (MPEG); Academy of Natural Sciences of Philadelphia, Philadelphia (ANSP); Carnegie Museum, Pittsburgh (CM); Field Museum of Natural History, Chicago (FMNH); Los Angeles County Museum of Natural History, Los Angeles (LACM); the Louisiana State University Museum of Natural Science, Baton Rouge (LSUMZ); the Museum of Vertebrate Zoology, Berkeley (MVZ); the National Museum of Natural History, Washington, D.C. (USNM); and the Peabody

Museum of Natural History, Yale University (YPM). A wing rule with a perpendicular stop at zero was used to measure flattened wing chord (wing), tail length (tail), breadth of the pale terminal tip to the rectrices (pale tip), and width of the central rectrix (central rectrix), and dial calipers were used to measure tarsus length (tarsus), culmen length from the anterior end of the nares to the tip (culmen), bill depth at the anterior end of the nares (bill depth), and bill width at the anterior end of the nares (bill width). All caliper measurements were made to the nearest 0.01 mm, those taken with the wing rule were made to the nearest 0.5 mm. General linear models were used to investigate gender-corrected differences among taxa for each of the characters measured. Residual diagnostics indicated no violations of the general linear model assumptions of error normality and constant variance. Plumage was described from specimens and compared to a standard color reference (Smithe 1975).

Results

Examination of our specimens and tape recordings, study of a large selection of museum specimens, extensive field observations that included reciprocal playback experiments, and discovery of multiple sites of sympatry without evidence of interbreeding convinced us that the two vocal types of yellow-bellied *Suiriri* represent distinct biological species. Furthermore, it is clear that the short-billed form that we collected from Mato Grosso is the same unnamed form that was first pointed out by Zimmer (1955) and later hypothesized to be a cryptic species by Traylor (1982). We propose to name this flycatcher

Suiriri islerorum sp. nov. Chapada Flycatcher

Holotype.—MPEG No. 54867, adult female from kilometer 2 on the road to Agua Fria, 15°25'S, 55°46'W, west of the town of Chapada dos Guimarães, approximately 720 m elevation, state of Mato Grosso, Brazil, collected 21 September 1999 by Dionisio Pimentel, tape-recorded by Kevin J. Zimmer. Voice specimen to be archived at Library of Natural Sounds (LNS), Cornell Laboratory of Ornithology, Ithaca, New York.

Diagnosis.—Similar in plumage and size to *Suiriri s. affinis* (Tables 1 and 2), but differs as follows: bill distinctly shorter, relatively broader, and more nearly uniform blackish (base of

Characters	S. islerorum	S. affinis	S. bahiae	S. suiriri
Culmen	8.0 ± 0.7	9.6 ± 0.6	8.5 ± 0.7	7.7 ± 0.4
	7.5-8.6 (23)	8.2-11.1 (61)	7.9-9.2 (3)	6.7-8.7 (108)
Bill depth	4.2 ± 0.3	4.6 ± 0.3	4.5 ± 0.9	4.2 ± 0.3
	3.7-4.9 (23)	3.8-5.4 (61)	4.5-4.6 (2)	3.7-4.9 (106)
Bill width	5.7 ± 0.3	5.4 ± 0.4	5.5 ± 0.1	5.0 ± 0.3
	5.1-6.3 (23)	4.7-6.1 (61)	5.4-5.6 (2)	4.4-5.6 (107)
Wing	82.6 ± 3.3	82.0 ± 4.4	77.2 ± 4.0	73.0 ± 3.3
0	72-87 (21)	70-88.5 (38)	73.5-81.5 (3)	65.5-81 (108)
Tail	71.5 ± 2.7	69.4 ± 3.8	66.7 ± 4.2	69.0 ± 3.6
	66-78 (21)	59-76 (38)	62-70 (3)	58-78.5 (108)
Tarsus	20.3 ± 0.7	20.5 ± 1.0	20.3 ± 0.7	19.8 ± 0.7
	19.1-21.7 (20)	17.2-22.5 (37)	19.8-21.1 (3)	17.9-22.1 (106)
Pale tip	6.4 ± 1.5	2.1 ± 1.5	1.2 ± 2.0	0.0 ± 0.0
1	3-11 (23)	0.0-4.8(61)	0.0 - 3.5(3)	0.0 (108)
Central rectrix	10.5 ± 1.1	8.6 ± 1.3	7.0 ± 1.0	<u> </u>
	8-12 (21)	6-11 (38)	6-8 (3)	—

TABLE 1. Measurements (mm) of *Suiriri islerorum* and congeners. Values are means \pm standard deviation followed by ranges, with sample size in parentheses.

mandible fleshy-pink in many specimens of *affinis*, particularly in females); dorsal surface of most of tail darker, more blackish-brown (browner, between Fuscous, color #21, and Vandyke Brown, color #121, in *affinis*); pale terminal fringe to tail broader and more highly contrasting (either absent, or, if present, narrow and weakly contrasting in *affinis*); both webs of outer rectrices more extensively pale, and dark subterminal patch on inner web of outer rectrices distinctly smaller; central rectrices broader and without paler edges; white of throat extends farther up on sides of face (to the gape in *S. islerorum*; only to the bottom of the bill in all *S. s. affinis* examined). *Suiriri islerorum* differs further from specimens of *S. s. bahiae* in having the grayish crown and nape less sharply demarcated from the greener back; back darker and less distinctly green; breast less whitish; rump and uppertail coverts more contrastingly pale; and central rectrices broader and not pale-edged. *Suiriri islerorum* differs from *S. s. suiriri* as follows: distinctly larger overall with proportionately shorter, broader tail; belly, flanks, thighs, and crissum yellow rather than white; undertail with a broad, contrasting pale

TABLE 2. Means \pm SD (sample sizes in parentheses) of measurements (mm) of *Suiriri islerorum* and *S. s. affinis* by sex, followed by a statistical comparison of the means of the pooled samples (both sexes) for each species. Values of *P* (= probability of a greater value of *F*) derived from Analysis of Variance (ANOVA).

	isler	orum	affi	inis	
Characters	Males	Females	Males	Females	Р
Culmen	8.1 ± 0.4	8.0 ± 0.3	9.8 ± 0.5	9.3 ± 0.5	< 0.0001
Bill depth	(6) 4.2 ± 0.4	(16) 4.2 ± 0.3	(31) 4.7 ± 0.3	(26) 4.6 ± 0.4	< 0.01
Bill width	5.8 ± 0.4	(15) 5.6 ± 0.2 (15)	(31) 5.5 ± 0.3 (31)	(26) 5.3 ± 0.4 (27)	< 0.01
Wing chord	85.1 ± 0.7	81.6 ± 3.6	85.0 ± 2.3	(27) 78.6 ± 3.8 (17)	< 0.05
Tail	71.2 ± 1.6	71.0 ± 2.7	70.9 ± 2.9	67.8 ± 4.1	< 0.01
Tarsus	21.2 ± 0.6	20.0 ± 0.06	21.2 ± 0.6	19.7 ± 0.8	NS
Pale tip	6.9 ± 0.8	6.2 ± 1.7	2.2 ± 1.5	2.2 ± 1.6	< 0.0001
Central rectrix	9.6 ± 1.1 (5)	10.9 ± 0.9 (16)	8.8 ± 1.2 (18)	8.3 ± 1.3 (17)	< 0.0001



FIG. 1. Displaying pair of *Suiriri islerorum*: female in foreground with wings raised. Key morphological features that distinguish this species from *S. s. affinis* can be seen in this photo: the short, thick bill, and the broad, pale, terminal fringe to the tail. Photographed near Cuiabá, Mato Grosso, Brazil on 22 September 1999 by Kevin J. Zimmer.

base (underside of tail in S. s. suiriri entirely dark except for contrastingly pale narrow outer web of outer rectrix on each side and pale shaft of outer rectrices); central rectrices distinctly broader and not narrowly pale-edged on either web; inner web of outer rectrix pale-based and pale-tipped, not entirely blackish; broader gray band across the breast; less extensively dark auriculars; and less distinct white supraorbital brow. Suiriri islerorum differs from both Sublegatus modestus and Sublegatus arenarum as follows: markedly larger; greener upperparts showing more contrast between nape and back (browner with little or no contrast in Sublegatus); rump and uppertail coverts contrastingly paler than back (no contrast in Sublegatus); upperside of tail blacker (less brown) with a pale base to the rectrices; throat contrastingly white. The new species differs from most members of Elaenia in lacking elongate crown feathers and a contrastingly colored, concealed coronal patch, as well as in having an entirely blackish bill. The contrastingly pale rump and base of the tail are characters not found in Elaenia.

Description of holotype.—See Figure 1 and color plate. Capitalized color names and numbers are from Smithe (1975). Forecrown brownish gray, closest to Hair Brown (color #119A), suf-

fusing into a grayer hindcrown and nape, closest to Glaucous (color #79). The gravish nape grades into an Olive (color #30) back and scapulars. Uppertail coverts and rump contrastingly paler than back, between Light Drab (color #119C) and Smoke Grav (color #45). Auriculars concolor with hindcrown, perhaps slightly duskier. Malar region between whitish and Pale Neutral Gray (color #86). Lores slaty. A narrow, pale, supraorbital brow extends to the forehead. Four long rictal bristles on both sides of gape, the longest 8.0 mm. Wings generally dusky, closest to Vandyke Brown (color #221), but secondaries narrowly pale-edged (closest to Light Drab, color #119C) on outer web. Basal portion of inner web of all remiges broadly pale-edged, between Pale Horn (color #92) and Drab-Gray (color #119D). Greater and median secondary coverts broadly tipped Light Drab (#119C), forming two distinct wingbars. Axillaries and underwing linings pale Sulphur Yellow (color #57).

Chin and throat whitish, grading posteriorally into Pale Neutral Gray (color #86). Center and sides of breast Glaucous (color #80), separating whiter throat from Sulphur Yellow (color #57) belly, flanks, thighs, and undertail coverts. Most of exposed dorsal surface of tail dark, between Dusky Brown (color #19) and Dark Gravish Brown (color #20). Contrasting paler band at tips of rectrices between Drab (color #27) and Dark Drab (color #119B); that paler tip 7 mm in length on central rectrix. Base of both webs of outer rectrices, and base of inner web of all other rectrices contrastingly pale, closest to Cream color (#54). That paler base to tail mostly concealed from above by uppertail coverts, but visible from below as a wide (35 mm) pale base that contrasts with a dark central panel (closest to Vandyke Brown, color #221), which in turn, contrasts with the pale terminal fringe. Basal portion of the shafts of most rectrices are closest to Pale Horn (color #92); those of the central rectrices are closer to Salmon (color #6). Outermost rectrix on each side has the outer web almost entirely pale, with a dark subterminal patch (26 mm in length) on the inner web. The pale outer web of the outer rectrix, in combination with the pale base to the rectrices and the pale terminal fringe, isolate and outline the dark central panel on the underside of the tail.



FIG. 2. Distribution of *Suiriri islerorum* and its congeners as confirmed by examination of specimens or tape recordings: black circles = *S. islerorum*; diamonds = *S. s. affinis*; circles touching diamonds = sites where *islerorum* and *affinis* are sympatric; squares = *S. s. suiriri*; plus signs = sites where *affinis* and *suiriri* are sympatric; and triangles = *S. s. bahiae.* "T" next to a symbol indicates the type locality for that taxon. "T" next to a circle-diamond locates Chapada dos Guimarães, Mato Grosso, Brazil, the type locality for *S. islerorum*. Note that no type locality is located for *S. s. bahiae*, which was described from a trade specimen whose only locality was "Bahia." Map by Morton Isler.

Soft parts in life: iris, medium brown; maxilla, black; mandible, basal one-quarter slaty gray, remainder black; lining of the mouth, yellow-orange; tarsus and toes, black; soles of feet and toes, paler gray; nails, black.

Measurements of holotype.—Culmen from anterior edge of nares, 7.8 mm; bill depth at anterior edge of nares, 4.4 mm; bill width at anterior edge of nares, 5.8 mm; wing chord, 85 mm; tail, 73 mm; tarsus, 20.1 mm; body mass 22.8 g. Ovary, 6×3 mm; oviduct, 3 mm wide; largest ovum, 4 mm.

Geographic distribution.—Locally distributed in cerrado and campos habitats throughout much of central Brazil, south of the Amazon and east of the Rio Madeira, and at least sparingly to depto. Santa Cruz, eastern Bolivia (Fig. 2). Most confirmed records are from Mato Grosso, Brazil, with scattered specimens east and north to the Brazilian states of Pará, Goiás, Tocantins, and Maranhão. The westernmost records are from Campo do Estanho, Amazonas, Brazil (M. Cohn-Haft tape recording), and Parque Nacional Noel Kempff Mercado, depto. Santa Cruz, Bolivia (LSUMZ 150871). Undoubtedly occurs more extensively within the area bounded by those records, but probably overlooked due to morphological similarity to *S. s. affinis*.

Elevational distribution.—The only specimens of Suiriri islerorum with elevational data on the labels are the ones that we collected in Mato Grosso, Brazil. Those range from 250 m on the Coxipo do Ouro Road near Cuiabá, to 720 m on the Agua Fria Road near Chapada dos Guimarães. That elevational range also encompasses all of our records that have been documented by tape recordings. The Bolivian specimen (LSUMZ) was from 450 m (J. Bates pers. comm.). Paynter and Traylor (1991) provide elevations for several of the sites from which S. islerorum were collected by other workers. Those should be viewed as pertaining to general collecting localities, and may not apply specifically to sites where Suiriri were collected. Including those data would extend the probable elevational range of S. islerorum from 150 m at Tocantinia, Tocantins, Brazil (LACM 46004) to 1200 m at São João da Aliança, Goiás, Brazil (LACM 40087).

Specimens examined: Skins.—Only specimens measured are listed. Plumages of all sympatric species of Elaenia and Sublegatus were compared superficially. Suiriri islerorum: Brazil, Mato Grosso, six males and nine females (MPEG 54865 to 54874, and 19299; AMNH 127882, 127883, 33101, and 33135); Goiás, three females (LACM 460087 and 40089, MPEG 19299); Maranhão, one female (FMNH 63435); Pará, one female (MPEG 49036); Tocantins, one female (LACM 46004); Mato Grosso do Sul, one unsexed specimen (ANS 159808). Bolivia, depto. Santa Cruz, one female (LSUMZ 150871). Of those, four males and six females (MPEG 54865 to 54874) were collected by us in Mato Grosso, Brazil.

Suiriri suiriri affinis: Brazil, Amapá, 10 males and 9 females (MPEG 46607 to 46619, AMNH 33100, USNM 515199); Goiás, five males, six females and two unsexed specimens (LSUMZ 31774, 67522, 67523; ANS 186661; USNM 516085; MPEG 22013; FMNH 344593 to 344595 and 75099; LACM 46003, 40090, and 40088); Mato Grosso, seven males and six females (MPEG 54875 to 54884, AMNH 33100, 33131, and 33133); Maranhão, one male and five females (FMNH 63431, 63432, 63434; MPEG 43526 to 43528); Minas Gerais, one male and two females (MPEG 36210, FMNH 56657, LACM 40086); Tocantins, one male (LACM 46005); Ceará, one male (USNM 264644); Piauí, one unsexed specimen (MPEG 50917). Bolivia, depto. Santa Cruz, three males (LSUMZ 124634, 124642, 150872). Of these, six males and four females (MPEG 54875 to 54884) were collected by us in Mato Grosso, Brazil.

Suiriri suiriri bahiae: Brazil, Bahia, one male and two females (LACM 37067 and 37068, FMNH 64119).

Suiriri suiriri suiriri: Argentina, Entre Rios, seven males, five females, and one unsexed specimen (YPM 66068 to 66073 and 83326, CM 140482, 140489, 140490, 140670, 140806, and 140867); Misiones, five males and five females (LSUMZ 56714 to 56723); Tucuman, three males, four females, and two unsexed specimens (FMNH 58012, 58019, 58369, and 58377; USNM 284898, 285001, 285002, and 285109; YPM 24195); La Pampa, one male and two females (USNM 284329, 284332, and 284335); Chaco, one male and one female (USNM 284330 and 284334); Buenos Aires, two males (USNM 55681 and 55683); Salta, one male (CM 45839); and Santiago del Estero, one male (MVZ 108323). Bolivia, Santa Cruz, 18 males, 14 females, and 1 unsexed specimen (CM 119820, 120212, 120213, 32786, 32787, 32831, 32889, 32891, 32952, 51402, 78970, 79244, 80363, and 80364; FMNH 181493, 181502, 181506, 294367, 295413, 296295, 296298, 296301, 335151, and 335152; LSUMZ 124633 to 124637, 153757, and 153758; YPM 31816 and 31817); Tarija, five males and three females (ANS 138951, 138952, 138954, 138955, 138958, and 138959; FMNH 294369 and 294370); Cochabamba, one male and two females (FMNH 181498 and 181500; ANS 136168). Paraguay, depto. Presidente Hayes, two males (MVZ 168120 and 168121); depto. Chaco, four males (FMNH 153007, 153010 to 153012). Brazil, Mato Grosso do Sul, one male and two females (FMNH 64121 to 64123); Parana, one male and one female (USNM 16367 and 16368). Uruguay, Represa Palmar, one male (ANS 187738).

Specimens examined: Tape recordings.—Data for recordings reproduced as sonograms are

provided in the corresponding figure legends. All recordings by Kevin J. Zimmer unless otherwise indicated. Suiriri islerorum: Brazil, Mato Grosso, west of Chapada dos Guimarães along the road to Agua Fria, 20 specimens, and Coxipo do Ouro road near Cuiabá, 8 specimens; Amazonas, 160 km E-SE of Humaita, 1 specimen (M. Cohn-Haft). Suiriri suiriri affinis: Brazil, Amapá, 12 specimens; Goiás, 2 specimens (A. Whittaker); Mato Grosso, west of Chapada dos Guimaraes along the road to Agua Fria, 4 specimens, and Coxipo do Ouro road near Cuiabá, 24 specimens. Bolivia, depto. Santa Cruz, 1 specimen (T. A. Parker, LNS 52044). Suririri suiriri bahiae: Brazil, Pernambuco, near Lagoa Grande, 16 specimens. Suiriri suiriri suiriri: Argentina, Salta, three specimens (S. Hilty). Bolivia, depto. Santa Cruz, one specimen (T. A. Parker, LNS 33629). Brazil, Rio Grande do Sul, one specimen (W. Belton, LNS 19531). Paraguay, Chaco Province, one specimen (D. Finch, LNS 57891).

Etymology.—We take great pleasure in naming this species after our good friends and colleagues, Morton and Phyllis Isler, in recognition of their numerous contributions to Neotropical ornithology. Mort and Phyllis authored a landmark monograph on tanagers (Isler and Isler 1987), and they have made pioneering contributions in developing methodologies for the analysis of vocal characters to assess species limits in antbirds and other suboscines (Isler et al. 1997, 1998, 1999). Their work on antbirds has served to heighten awareness of the importance of vocalizations as taxonomic characters in all suboscine groups, and as such, has far-reaching implications for the accurate assessment of regional endemism and biodiversity, and, ultimately, for conservation. The Islers have contributed greatly to our own studies of Neotropical birds, and are constant sources of advice, encouragement, and help. The English name calls attention to the type locality, the Chapada dos Guimarães, Mato Grosso, Brazil, which is an important reservoir of threatened cerrado flora and fauna.

Remarks

Sexual dimorphism and variation in the type series.—The type series of Suiriri islerorum consists of 23 adult specimens (6 males, 16 females, and 1 unsexed specimen). Males resemble females, and plumage variation among paratypes appears to be neither sexually nor geographically influenced. There is some individual variation in color of the uppertail coverts and in the extent of the contrastingly pale base of the rectrices. Compared to the holotype, some individuals (MPEG 54872, LACM 46004, LSUMZ 150871, AMNH 127882) are more greenish-yellow (closest to Citrine, color #51) on the uppertail coverts, another (MPEG 54870) was buffier, and two (MPEG 54871 and FMNH 63435) had the uppertail coverts nearly the same color as the back. Two specimens (MPEG 54865 and LACM 40087) are more extensively gray dorsally, with the mantle and lower back more nearly concolor with the nape. Similar variation in rump-lower-back contrast was apparent among the 61 specimens of S. s. affinis examined.

Most observed variation among paratypes was related to feather wear and molt condition. Most specimens are browner on the forecrown and grayer on the hindcrown, but a few are more uniformly gray throughout the crown. Individual feathers of the forecrown have a brownish longitudinal streak along the shaft, and are gray around the fringe. When those feathers are worn, the extent of the gray relative to the brownish central streak is reduced, and the forecrown assumes a more brownish tinge. Freshly molted birds had grayer forecrowns. Similarly, variation in the breadth of the pale terminal fringe to the rectrices, the buffy tips of the secondary coverts, and the pale edges of the remiges all was influenced by wear.

One male specimen (MPEG 54871) had an unusually long tip (hook) to the maxilla. The culmen measurement for that bird was 8.52 mm, but without the tip the culmen would measure 7.64 mm. In general, males were slightly larger than females, although bill measurements were nearly identical (Table 2).

Breeding and molt.—Ten of the 23 specimens of Suiriri islerorum (MPEG 54865 to 54874) were collected from Mato Grosso, Brazil between 20–22 September 1999. All had enlarged gonads, and two females (MPEG 54866 and 54872) had well-developed brood patches. All were vocal and territorial. Most birds showed signs of moderate to heavy wear of the secondary coverts and rectrices. Similarly, the FMNH specimen from Maranhão was collected 2 September 1925, and showed moderate to heavy wear. We believe that all of those birds were in breeding condition. We never have observed family groups of *S. islerorum* during our August and September visits to Mato Grosso. That, combined with the apparent breeding readiness and territorial nature of the birds we collected in late September, suggests that the main hatching and fledging period is probably in October. That would fit a common pattern for insectivorous birds in regions with pronounced dry seasons, in which hatching coincides with onset of the rainy season and the concomitant flush of insect populations (Walsberg 1977, Marr 1981, Zimmer 1993).

The four AMNH specimens from Mato Grosso were collected between 7 February and 26 May. All had remiges and rectrices that were less worn and more broadly pale-eged or fringed than in our specimens. Similarly, the three LACM specimens from Goiás and Tocantins were collected between 14 April and 3 May, and all were in fresher plumage than our series from Mato Grosso. The ANSP specimen (ANSP 159808) was collected 30 June and was in fresh condition. The LSUMZ specimen (LSUMZ 150871) was collected 29 August, and was in fresh condition with a trace of molt on the head and with an ovary that measured 6×7 mm. The condition of those specimens suggests that S. islerorum undergoes one molt sometime after breeding in September to October, and then probably undergoes at least a partial molt again in spring or summer prior to the next breeding season.

Vocalizations.--Male and female Suiriri islerorum have different loudsongs, which are typically delivered as sex-specific elements of simultaneous duets, but are occasionally delivered separately. The male loudsong (Fig. 3A) is a loud series of paired couplets, all notes having a distinctly twangy quality. The song has two discernible phrases that are repeated in predictable patterns (where where, whooz it whooz it, where where whooz it, whooz it, whooz it, whooz it). Sometimes males will sing a series of "whooz it" notes without the "where where" notes. The number of consecutive "whooz it" couplets may vary from two to six (rarely more), but no more than one "where where" couplet seems to be given without interjecting the "whooz it" notes. In response to playback, males frequently sing longer songs. The most commonly heard male calls are isolated notes



FIG. 3. Vocalizations of *Suiriri islerorum* recorded from Mato Grosso (MT), Brazil. MPEG numbers in parentheses match tape recordings with specimens in the Museu Paraense Emílio Goeldi, Belém, Pará, Brazil. (A) Male loudsong (MT, near Cuiabá, 22 September 1999). (B) Male (MPEG no. 54874) calls (MT, Chapada dos Guimarães, 21 September 1999). (C) Female loudsong (MT, near Cuiabá, 22 September 1999). (D) Female (MPEG no. 54872) *"wheer-deer"* call (MT, Chapada dos Guimarães, 21 September 1999). (E) Female *"zhuwheep"* and *"zhuwheep-oo"* calls (MT, near Cuiabá, 22 September 1999). All recordings by Kevin J. Zimmer.

or couplets similar to those given in loudsongs (Fig. 3B). The female loudsong (Fig. 3C) is a loud, bubbly rattle of variable length that is typically preceded by one or two well-differentiated "whur" or "wheer" notes. In response to playback, females typically lengthen the rattle element of their songs. Females commonly give two types of calls. The first is a series of "wheerDEER" calls (Fig. 3D) that are somewhat similar to the male couplets, but that are more emphatic (particularly on the second syllable), with a less twangy, less strident quality, which are frequently interjected into duets. Outside of duets, the most commonly heard female call is a querulous sounding, two-or-three-syllabled "zhuwheep" or "zhuwheep-oo," in which the long first note is diphthongal and distinctly upward-inflected at the end, and the second, shorter note, when present, drops in frequency (Fig. 3E). That call is typically given in the context of a contact call when a female is visually separated from her mate. In duets (Fig. 4), the male and female sing their loudsongs simultaneously, creating a somewhat discordant jumble of notes, with the female rattle and the twangy male notes equally distinct.

As with S. islerorum, the male and female loudsongs of S. s. affinis are most commonly heard as sex-specific elements of simultaneous duets, but are sometimes delivered separately. The male loudsong of S. s. affinis is a series of sneezy "pi-chew" notes, variable in length, that typically begins with several squeaky introductory notes and ends with several one-syllabled "chew" notes (Fig. 5A). The female loudsong (Fig. 5B) is a series of loud, squeaky notes that typically decelerates noticeably toward the end. Those notes are similar in quality to the introductory notes in male songs, but are higher frequency, higher amplitude, and more widely spaced. The terminal notes in a female loudsong often drop in frequency. Females have a variety of single-note calls, most of which are nasal and have a distinctly whiny quality (Fig. 5C, D). Those are routinely uttered as contact calls, but when a female gives several differentiated whiny calls in rapid succession ("suiree, swee, swiroo, chew") it is usually the



FIG. 4. Male-female duets of *Suiriri islerorum* recorded from Mato Grosso (MT), Brazil. MPEG numbers in parentheses match tape recordings with specimens in the Museu Paraense Emílio Goeldi, Belém, Pará, Brazil. (A) male-female (MPEG nos. 54865 and 54866) duet (MT, near Cuiabá, 20 September 1999). (B) Male-female (MPEG nos. 54874 and 54872) duet (MT, Chapada dos Guimarães, 21 September 1999). (C) Male-female (MPEG nos. 54869 and 54867) duet (MT, Chapada dos Guimarães, 21 September 1999). The female from this pair (MPEG no. 54867) is the holotype for the species. All recordings by Kevin J. Zimmer.

synchronizing cue that begins a duet. A female, whose mate we had collected, repeated those single-note nasal calls for more than an hour afterwards. The most frequently heard male call outside of a duet context is a single-note, somewhat guttural "werk" (Fig. 5E). Less commonly heard is a low-frequency rattle that may function as an aggression call (Fig. 5F, G). We have heard that call given several times from birds of unknown sex within foraging family groups, as well as from a female that was attempting to aggressively displace a Lesser Elaenia (Elaenia chiriquensis) from a fruiting tree. In duets (Fig. 6), the higher amplitude female loudsongs tend to mask the male loudsongs. The similarity of the female notes to the introductory male notes makes it even more difficult to distinguish the full male song.

All vocalizations of *S. s. bahiae* appear to be homologous to the vocalizations of *S. s. affinis.*

The male loudsong of S. s. bahiae begins with a rapid series of squeaky, somewhat run-together notes that drop in frequency before yielding to a distinctive series of "pitty-chew" elements (Fig. 7A). The introductory series recalls the sounds that would be made by squeezing a toy rubber duck several times in rapid succession. The female loudsong (Fig. 7B) is a series of squeaky "choop" notes (peak frequency of about 8 kHz) delivered at about 8 to 10 notes per second. Those notes are similar in tonality to those that precede the "pitty-chew" elements in the male song, but are higher in frequency, more widely separated, and do not drop in frequency through the series. Both sexes give their respective songs during simultaneous duets (Fig. 6D). In duets, the female loudsong is typically louder than that of the male. A single duet bout might include two or more songs from each bird, with the final female song in the bout often decelerating noticeably toward the end of the song. The terminal notes in such a decelerated series are lower in frequency than the introductory notes. Males frequently conclude duets with a few sputtering "pitty-chew" calls. Outside of duets, the most frequently heard male call is a guttural, single note (Fig. 7C). This call apparently functions as a contact call. The series of "pitty-chew" calls also is frequently given independent of the squeaky prelude (Fig. 7D), particularly in duets. The most commonly heard female call is a nasal "nyew" with a distinctly whiny quality. Those calls are typically delivered singly in the context of contact calls, but they also are often strung together in rapid succession (Fig. 7E), particularly by birds agitated by tape playback. Females responding to playback typically begin giving those whiny notes in flight as they approach the sound source. As in S. s. affinis, a rapidly delivered series of those female notes following playback appears to be the synchronizing cue that precipitates the responsorial duet from the pair. The only vocalization of S. s. affinis for which we could find no homolog in S. s. bahiae was the rattle call (Fig. 5F,G). The apparent absence of such a vocalization in S. s. bahiae may be an artifact of sampling, because rattle calls were only occasionally recorded from S. s. affinis.

Our inventory of tape recordings of nominate S. s. suiriri is small. What appears to be a loudsong in Argentina (Fig. 8A) is a long (3 to 5 s), frenetic, sputtering series of nasal notes that rise and fall in frequency, with occasional differentiated querulous notes scattered through the middle. We do not know if this loudsong is specific to one sex, and, if so, to which one. The most common vocalization is a single nasal "rowl" or "jyow" note that is repeated incessantly for prolonged periods. Minor variations of this call have been recorded from Argentina, Brazil, Bolivia, and Paraguay (Fig. 8B-E). Another call recorded from Paraguay is a 2–3 s rattle at about 5–6 kHz (Fig. 8F).

Duet display behavior.—The most striking behaviors of *S. islerorum* were those associated with territorial duets of mated pairs (Fig. 1 and color plate). Pairs were tightly synchronized in their duets. The first few notes of either a male or female loudsong were enough to initiate most duets, with the second bird joining in immediately. Prior to singing, pairs typically assumed a prominent perch in the crown of a tree or on a bare snag, usually within 0.5 m of one another. Duets were always accompanied by dramatic, sex-specific, stereotyped motions. The male flicked both wings high above his back (the wings nearly touching) at a rate of about one per second for the duration of the duet (6-10 s). With each downstroke of his wings, he flipped his tail upwards, at about a 45° angle. When the wings were once again flicked upwards, the tail was flipped down 30 to 45° below the horizontal. During the display, the male leaned forward, so that his rump was held at about the same plane as his head. The tail was fanned throughout much of the display, emphasizing the contrast between the yellowish-buff base and the blackish distal half. Some males rotated at approximately a quarter turn with each up-and-down cycle of the wings and tail, such that they were constantly turning in circles while displaying. Simultaneous with the male's display, the female also raised her wings high above her back, but held them there, fullyfanned, for about 2-3 s at a time before lowering them gradually. Females repeated that motion two or three times during each duet. At the same time that a female was raising her wings, she would also fan and dip her tail downward at a 20 to 45° angle, flipping the tail back up to the horizontal position as the wings were lowered. The fanning of the wings by females accentuated the largely pale inner webs of the remiges such that backlit birds appeared to have translucent wings. Females also frequently rotated while displaying, but were less likely to do so than the frenetic males. Females also maintained a more upright posture throughout their displays. Those displays of S. islerorum accompanied each of the more than 200 duet bouts that we witnessed, and are remarkably similar to those of the Streamer-tailed Tyrant (Gubernetes yetapa) of southern South America, and, to a lesser extent, of White-bearded Flycatcher (Phelpsia inornata) of Venezuela (K. Zimmer pers. obs.).

We never have witnessed similar displays from either *S. s. affinis* or *S. s. bahiae*, in spite of having witnessed more than 200 duets of the former and more than 100 duets of the latter. Sick (1993) described the song of *S. s. affinis* as "repeated while lifting both wings vertically." That description almost certainly is based upon observations of *S. islerorum. Suiriri s. affinis* and



FIG. 5. Vocalizations of *Suiriri s. affinis* from various sites in Amapá (AP) and Mato Grosso (MT), Brazil. MPEG numbers in parentheses match tape recordings with specimens in the Museu Paraense Emílio Goeldi, Belém, Pará, Brazil. (A) Male (MPEG no. 54881) loudsong (MT, near Cuiabá, 22 September 1999). (B) Female loudsong (MT, near Cuiabá, 21 September 1998). (C) Female "whiny" calls (MT, near Cuiabá, 22 September 1999). (D) Female "whiny" calls (AP, north of Macapá, 12 February 1999). (E) Male guttural call (MT,



FIG. 6. Male-female duets of *Suiriri s. affinis* and *S. s. bahiae* from various localities in Amapá (AP), Mato Grosso (MT), and Pernambuco (PE) Brazil. (A) *S. s. affinis* from Chapada dos Guimarães, MT (21 September 1999). (B) *S. s. affinis* from Chapada dos Guimarães, MT (21 September 1999). (C) *S. s. affinis* from near Porto Grande, AP (7 February 1999). (D) *S. s. bahiae* from Lagoa Grande, PE (15 January 1997). All recordings by Kevin J. Zimmer.

S. s. bahiae exhibited identical behaviors when displaying. Duets almost always were initiated by several nasal, single-note female calls (Fig. 6A–D) given in rapid succession. If the male was in a different tree or another part of the same tree, he would rapidly fly toward the female, land next to her, and then the pair would simultaneously sing their respective loudsongs. The posture of both birds during duets was nearly horizontal, with the wings typically drooped slightly at the sides. Birds usually quivered their wings slightly while keeping

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Chapada dos Guimarães, 21 September 1999). (F) Rattle call from female (MT, near Cuiabá, 22 September 1999). (G) Rattle call of bird of unknown sex (AP, north of Macapá, 12 February 1999). All recordings by Kevin J. Zimmer.



Suiriri suiriri bahiae

FIG. 7. Vocalizations of *Suiriri s. bahiae* recorded near Lagoa Grande, Pernambuco, Brazil. (A) Male loudsong (25 January 1999). (B) Female loudsong (25 January 1999). (C) Male guttural call (25 January 1999). (D) Male "*pitty-chew*" calls (25 January 1999). (E) female "whiny" calls (25 January 1999). All recordings by Kevin J. Zimmer.



FIG. 8. Vocalizations of *Suiriri s. suiriri*. (A) loudsong (Argentina, Salta, 6 October 1987; S. Hilty recording). (B) Single-note call (Argentina, Salta, 6 October 1987; S. Hilty recording). (C) Single-note call (Brazil, Rio Grande do Sul, 50 km southwest Santo Antonio das Missões, 4 November 1975; W. Belton recording, LNS 19531). (D) Single-note call (Bolivia, depto. Santa Cruz, west of San Isidro, 6 October 1983; T. Parker recording, LNS 33629). (E) Single-note call (Paraguay, Chaco Province, Filadelfia, 21 August 1990; D. Finch recording, LNS 57891). (F) Rattle call (Paraguay, Chaco Province, Filadelfia, 21 August 1990; D. Finch record-INS 57891).

them drooped, and sometimes simultaneously shivered the tail up-and-down in a shallow arc of less than 5°. Unlike *S. islerorum*, neither *affinis* nor *bahiae* habitually selected prominent perches from which to display, and often duetted from within the canopy of trees. Birds responding to tape playback often sang as they were flying toward the sound source, a behavior that we did not observe in *S. islerorum*. On several occasions we had *affinis* males that were separated from their mates respond to tape playback by flying in and perching near us without vocalizing. Even after leaving and being brought back by tape playback two or three times, those males would not sing on their own. In each case, a female eventually flew in giving several nasal calls and the pairs immediately began to duet.

Tape playback experiments.—Playback experiments with Suiriri recordings offer further evidence of the significance of vocal differences among the taxa, and of their role as potential

	Response to playback of				
Locality	islerorum	affinis	bahiae	suiriri	
		S. islerorum			
Mato Grosso, Brazil	strong (11)	none (11)	none (11)	none (6)	
		S. s. affinis			
Amapá, Brazil	none (3)	strong (3)	strong (3)	none (2), moderate (1)	
Mato Grosso, Brazil	none (12)	strong (12)	strong (12)	—	
Totals	none (15)	strong (15)	strong (15)	none (2), moderate (1)	
		S. s. bahiae			
Pernambuco, Brazil	none (5)	strong (5)	strong (5)	none (3), strong (2)	

TABLE 3. Summary of playback trials (as detailed in the text) involving *Suiriri* flycatchers (*S. islerorum, S. s. affinis, S. s. bahiae* and *S. s. suiriri*). Numbers in parentheses indicate the number of pairs or family groups of the subject taxon that were tested for each stimulus taxon.

isolating mechanisms. We performed tape playback experiments on 11 pairs of Suiriri islerorum near Cuiabá and Chapada dos Guimarães, Mato Grosso, Brazil (six pairs in September 1998 and five pairs in September 1999). The six pairs in the 1998 trials were presented with recordings of S. s. bahiae from Pernambuco, Brazil, S. s. affinis from Cuiabá, Mato Grosso, Brazil, and S. s. suiriri from Argentina. The five pairs in the 1999 trials were presented with the same recordings of S. s. bahiae and S. s. affinis. None of the 11 pairs tested showed any response to tape playback of suiriri, affinis, or bah*iae* vocalizations. When presented with playback of prerecorded S. islerorum vocalizations, all 11 pairs responded by immediately approaching the sound source and duetting multiple times. In several cases, those birds flew in from >100 m away when responding to playback of their own vocalizations.

We performed tape playback experiments on 12 pairs or family groups of S. s. affinis near Cuiabá and Chapada dos Guimarães, Mato Grosso, Brazil (six pairs in September 1998 and four pairs and two family groups of four in September 1999). Birds in all 12 trials first were presented with taped vocalizations of S. islerorum from Chapada dos Guimarães, then with recordings of S. s. bahiae from Pernambuco, Brazil. None of the 12 pairs or family groups responded to playbacks of vocalizations of S. islerorum, but all 12 pairs of adults responded strongly to playback of S. s. bahiae vocalizations. We also performed tape playback experiements on two family groups and one pair of S. s. affinis north of Macapá, Amapá, Brazil (February 1999). Those birds first were presented with playback of S. islerorum recordings, to which none of them responded. We then presented them with playback of nominate *S. s. suiriri* from Argentina. The adult pair from the first family group responded by approaching the sound source and peering about on two occasions, but did not vocalize. None of the four birds from the other family group showed any interest in playback of nominate *S. s. suiriri*, nor did the lone pair. When presented with tape of *S. s. affinis* from Mato Grosso and *S. s. bahiae* from Pernambuco, all three pairs of adult *S. s. affinis* from Amapá responded strongly by approaching and duetting.

In January 1999, we performed tape playback experiments on five pairs of S. s. bahiae near Lagoa Grande, Pernambuco, Brazil. Those birds were first presented with taped vocalizations of S. islerorum from Mato Grosso, Brazil. None of the five pairs showed any response to those playbacks. We then presented them with playback of S. s. affinis from Mato Grosso. All five pairs responded strongly to playback of S. s. af*finis,* always approaching the sound source and duetting by the fourth playback. We also presented the five pairs of S. s. bahiae with playback of nominate S. s. suiriri from Argentina. Three of the pairs did not respond to the voice of nominate birds. The other two pairs responded strongly (approach and vocalizations), but it should be pointed out that they were previously stimulated by tape of affinis from Mato Grosso. The results of those playback trials are summarized in Table 3.

Foraging behavior and social structure.—Suiriri islerorum typically was encountered in closely associated pairs, apart from other species. They foraged mostly in trees (rarely descending to low shrubs or the ground), moving energetically with short pauses between hops and frequent and erratic changes of direction. They gleaned various small arthropod prey from leaf and branch surfaces. Once prey was spotted, they frequently used wing-assisted hops to close distance rapidly, then lunged forward for a horizontal capture, or jumped upward to glean a prey item from overhead. They also engaged in frequent darting aerial sallies upward or outward to glean prey from undersides of leaves or branches. Those sallies varied from 15 cm to 1 m and typically involved little true hovering. Those behaviors were similar to that of members of the genera Tolmomyias and Platyrinchus, although S. islerorum were more constantly in motion and were more agile and acrobatic in pursuing prey (K. Zimmer pers. observ.). Suiriri islerorum also made occasional longer (up to 2 m), looping sallies out from the crown or lateral branches of trees and back to pursue flying insects. Perch changes were usually followed by an obvious, but relaxed downward dip of the tail, similar to tail movements of Vermilion Flycatcher (*Pyrocephalus rubinus*).

Suiriri s. affinis in the same areas frequently perch-gleaned or hover-gleaned small fruits (particularly those of Curatella americana), although they spent more time in pursuit of arthropods. Suiriri s. affinis foraged mostly in relatively open trees, progressing by hops of 5 to 15 cm, primarily along main branches. Their movements through trees were generally more leisurely in pace (almost Vireo-like) and more predictable in progression than in *S. islerorum*. Birds paused for 2–15 s between hops to scan live foliage, fruit clusters, or bark surfaces. They generally worked from the interior of a tree outward, or from the subcanopy up, but without frequent changes of direction as in S. islerorum. Arthropod prey usually (~75% of all captures) were gleaned directly from leaf or branch surfaces by reaching out, up, or down. Foraging birds often picked directly at branch surfaces, particularly on trees with furrowed bark. They also frequently hover-gleaned prey by hovering 1–2 s beneath green leaves in the outer portion of the canopy. That was different from the darting sallies (with little or no true hovering) made by S. islerorum. Suiriri s. affinis often dropped 1-3 m from branches to the ground to pounce on prey spotted from above. That behavior was particularly common in recently burned or very open areas, and was similar to foraging techniques routinely employed by bluebirds (*Sialia* spp.; K. Zimmer pers. obs.) in North America. *Suiriri s. affinis* also made occasional short, looping sallies of 1–2 m out from crowns of trees in pursuit of flying insects, but that behavior was less frequent than in *S. islerorum*. Like *S. islerorum, affinis* periodically wagged its tail downward in a relaxed manner when foraging, particularly after perch changes. Foraging behavior of *S. s. affinis* observed in Amapá, Brazil was identical to that described above from Mato Grosso.

The social structure of *S. islerorum* requires further investigation. We have never encountered more than two birds together. However, in September 1999, we had two experiences that suggest that S. islerorum is at least occasionally polygynous. On 21 September 1999, we taped a pair of S. islerorum along the Agua Fria Road, Mato Grosso, Brazil. After obtaining voucher tapes, we collected the displaying female (MPEG 54867). The male flew a short distance out of sight. Immediately after retrieving the female, we broadcast more tape playback from the same spot, and a male returned. As soon as the male perched in front of us, a second bird flew into the same tree and sang a typical female loudsong. The male immediately chased that second female, pursuing her around trees and shrubs. This was repeated on five occasions; each time we presented tape playback of duets the male would approach, followed closely by the second female, which he would then aggressively drive off. Only once during those encounters did the two birds duet. On our last playback attempt, the male drove the female to the ground and appeared to mount her. They then flew to a nearby tree and performed more duets before we collected both birds (male MPEG 54869, second female MPEG 54868). Gonads of all three birds were enlarged.

Later on 21 September, we were collecting farther along the Agua Fria Road when we taped in another pair of *S. islerorum*. Once again, we collected the female (MPEG 54872) first, and the male flew off. After a few minutes we presented more playback of duet vocalizations. Immediately, a pair of *S. islerorum* flew into the same tree from which we had collected the female, and proceeded to duet multiple times. After obtaining voucher tapes, we collected both birds (second female MPEG 54873, male MPEG 54874). The first female had a conspicuous brood patch and the gonads of all three birds were enlarged.

In each of those instances, what we assumed to be the original male appeared to return with a second adult female in breeding condition within 5 min of the time that we had collected his previous mate, which suggests that those males had been mated to two birds all along. It seems highly unlikely that more than one male was involved in either case. There was no evidence of a second territorial male or pair in the vicinity prior to collection of the first females. Had we been at a boundary between two territories, it seems likely that our tape playback would have elicited responses from both neighboring pairs. Instead, playback brought an immediate approach and duet response from a single pair. Following our collection of the female of each pair, the respective males flew off out of sight, after which a male flew back from roughly the same area minutes later in response to further playback. Birds responding to the second round of tape playback perched in the same or adjacent shrubs as those used by the birds responding to the first tape playbacks. We have only rarely found pairs of S. islerorum occurring in close enough proximity to one another that we could hear (even distantly) two pairs from a single spot, making it even less likely that two independent territorial pairs were involved in each instance.

Systematic relationships.—Some generalizations regarding relationships among the yellow-bellied group of Suiriri can be made. Suiriri islerorum is sufficiently distinct to be considered a separate species under any of the widely accepted species concepts (McKitrick and Zink 1988). Vocal distinctions are particularly strong. Suiriri islerorum differs strikingly from nominate suiriri, affinis, and bahiae in its male and female loudsongs, duets, and in all known male and female calls. Duets serve multiple functions, including coordinated defense of territory and pair-bonding. In Suiriri, as in the majority of duetting species, the same types of duets are used during bouts of territorial defense, as a prelude to copulation, and when pairs reunite following visual separation (Farabaugh 1982, K. Zimmer pers. observ.). In sexually monochromatic species (Suiriri), sexual specificity of duet contributions probably serves in mate attraction as well as in identifying the sex of a territorial tresspasser (Farabaugh 1982). A likely byproduct of sexual specificity of duet roles is the strengthening of reproductive isolation. In an habitually duetting genus such as *Suiriri*, vocal differences between taxa would seem to present major obstacles to reproductive compatability. Further barriers would be presented by significant differences in stereotyped physical displays associated with the vocalizations. As detailed above, pairs of *S. islerorum* perform distinctive displays with each duet. Nothing that we have heard or seen in the vocal and display repertoire of *affinis* or *bahiae* suggests an approach to *islerorum*.

The biological and taxonomic significance of those differences is suggested by the results of our playback experiments. Although we were unable to perform all pairwise tests, the ones performed were unequivocal. None of the *affinis* or *bahiae* tested showed any response to repeated playbacks of *islerorum*, nor did any of the *islerorum* respond to playbacks of the other taxa.

Morphological differences from affinis and bahiae are subtle yet distinct, even when observed in the field. Among the eight characters that were measured, Suiriri islerorum differed significantly from affinis in culmen length, bill width, bill depth, wing chord, tail length, width of the central rectrix, and width of the pale tip to the rectrices (Table 2). The two species also differed in the color pattern of the outer rectrices, and in whether or not the central rectrices were pale-edged. Our sample of affinis indicated substantial sexual dimorphism in bill size and color of the mandible, whereas no such dimorphism was apparent in *islerorum*. It is not known whether juveniles of S. islerorum share the unique spotted pattern to the upperparts found in juveniles of other Suiriri.

Most important, *Suiriri islerorum* and *S. s. affinis* are syntopic at multiple sites, and show no evidence of interbreeding. At the two localities in Mato Grosso, Brazil, where we conducted field studies, both forms were relatively common and all pairs of *Suiriri* were assortatively mated by vocal type and morphological type (as confirmed by tape recordings, specimens, and tissue samples). Thus, they meet the primary criteria for being considered species under the biological species concept. Finally, preliminary molecular analyses of tissue samples indicates that *S. islerorum* is strongly differentiated genetically from both *S. s. affinis* and *S. s. bahiae* (J. Bates pers. comm.). Those results will be presented elsewhere as part of an overview of genetic diversity in *Suiriri*.

Based on vocal similarities, S. s. affinis and S. s. bahiae clearly are closely related. The latter form resembles the former in having a long bill and yellow belly, but differs in being shorterwinged, showing little back-rump contrast, and in lacking the contrasting pale base to the rectrices (Traylor 1982). However, our examination of 61 specimens of affinis suggests that the degree of back-rump contrast and the extent of the contrasting pale base of the rectrices are individually variable characters, and extreme examples of affinis may at least approach typical examples of bahiae. Hayes (2001) also found significant plumage variability in specimens of bahiae. All vocalizations of bahiae appear to be homologous to those of affinis, and display behaviors of duetting pairs are identical. Furthermore, in reciprocal tape playback experiments, all pairs of bahiae responded strongly to playback of affinis vocalizations, as did all pairs of affinis to vocalizations of bahiae.

The relationship of nominate S. s. suiriri to the yellow-bellied forms remains uncertain. Nominate birds are strongly differentiated morphologically and vocally from *islerorum*, and in tape playback experiments, the latter species did not respond to playback of suiriri vocalizations. There is no reason to consider them as anything other than separate species. In the absence of contact, nominate birds also would appear to be sufficiently distinct from affinis and bahiae in both morphological and vocal characters as to warrant separate species status. However, the status of intergrades or hybrids from the contact zone in northern Paraguay and southwestern Brazil remains an issue. Hayes (2001) found that presumed hybrids from the contact zone had plumage characters intermediate between suiriri and affinis, and exhibited significant plumage variability. The apparent scarcity of parental phenotypes from within the contact zone suggested that the two forms were freely interbreeding, and therefore, conspecific (Hayes 2001). Further uncertainty is introduced by our playback experiments, in which some pairs of affinis and bahiae

responded to *suiriri* vocalizations, whereas most pairs showed no response. More comprehensive inventories of tape recorded vocalizations of nominate birds are needed for a proper vocal analysis. Also needed are field studies from the contact zone between *suiriri* and *affinis*, as well as more extensive playback experiments focused on this pair of taxa. Molecular analyses in progress (J. Bates et al. unpubl. data) also should clarify those relationships.

Ecology and conservation.—Suiriri islerorum is a bird of the cerrado region, a biogeographic region that encompasses 1.5 to 2 million km² centered on the Brazilian shield, with extensions into eastern Bolivia and northeastern Paraguay (Eiten 1972). The term "cerrado" has been applied generally to virtually all of the nonforest habitats of that region, although geographically it varies greatly in species composition and physiognomy. Five major subtypes of cerrado have been recognized by botanists (Eiten 1972). Of those, we have found Suiriri islerorum to occur in three: (1) cerrado sensu stricto, woodland with closed scrub and scattered trees; (2) campo cerrado, more open scrub with a few trees; and (3) campo sujo, grassland with scattered shrubs and few trees. In the Chapada dos Guimarães and Cuiabá regions of Mato Grosso, Suiriri islerorum is locally fairly common in some areas but seemingly absent from others. Moderately closed, shrubby areas with a significant grass component and scattered trees 2-5 m tall (as exemplified by the first several kilometers of the Agua Fria road near Chapada dos Guimarães) have the highest densities of S. islerorum. Our limited surveys have averaged 1 to 2 pairs per kilometer of road, but more extensive dawn surveys using systematic tape playback undoubtedly would yield higher densities. The species is somewhat less common along the Coxipo do Ouro road near Cuiabá, where the habitat is more wooded with pockets of regularly spaced trees (closer to cerrado sensu stricto; Eiten 1972). Suiriri s. affinis occurs alongside *islerorum* in both areas, but is more common in the more open woodlands and less common in the shrubbier, grassier cerrado.

The areas in which we have found *Suiriri islerorum* are subject to regular human perturbation. The biggest disturbance during the tenure of our work has been fire. Accidental or deliberately set fires have burned significant portions of cerrado along the Agua Fria road in three of the last five years, and have also affected the nearby national park. Local populations of both *Suiriri islerorum* and *S. s. affinis* have persisted in heavily burned areas, but the repeated burning of the same areas without sufficient time for recovery of the shrub community likely will have a negative effect. Housing developments have spread into the cerrado along the Agua Fria road, and continued expansion soon will threaten the type locality of *islerorum*.

On a broader scale, the dry forest and grassland habitats of central South America are considered both among the most endangered and unique biomes in the Neotropics (Stotz et al. 1996). The cerrado is especially threatened, with more than 75% of the 41 endemic birds considered at risk, and more than 45% considered either threatened or endangered (Stotz et al. 1996). The primary threat derives from the wholesale mechanized conversion of native cerrado and campo communities to large-scale agriculture, particularly soybeans. The dryseason practice of annually burning open country habitats for small-scale agriculture, deeply ingrained among most rural populations, is a secondary threat whose long term environmental consequences have only recently raised widespread concern.

Before the true conservation status of Suiriri islerorum can be assessed, we first need a more complete understanding of its distribution. We expect that it will eventually prove to be broadly sympatric with S. s. affinis throughout much of the cerrado region. At present, Suiriri islerorum is known to occur in two large national parks, Chapada dos Guimarães National Park, Mato Grosso, Brazil, and Noel Kempff Mercado National Park, depto. Santa Cruz, Bolivia. Both parks contain extensive areas of seemingly suitable cerrado habitat, and should be systematically surveyed to assess densities of Suiriri islerorum and other cerrado endemics. Another protected area that should be surveyed for islerorum is the Reserva Ecológica Serra das Araras in western Mato Grosso, Brazil.

The need for adequate surveys of endangered cerrado habitats has been pointed out by others (Bates et al. 1992, Silva 1995, Parker and Willis 1997), but its importance cannot be overstated. Lack of understanding of species limits in widespread, polytypic groups, along with incomplete knowlege of distributions may result in the serious underestimation of regional and local biodiversity and endemism. Such miscalculations could have serious repercussions when important conservation priorities are being set. In an analysis of the intensity of collecting efforts in the cerrado region, Silva (1995) found that roughly 70% of the cerrado region did not meet the criteria of having been "minimally sampled" for birds. It is instructive that Suiriri islerorum occurs in at least seven of the sites that met Silva's requirements for being satisfactorally sampled, including three regions (Goiânia, Cuiabá, and Parque Nacional Noel Kempff Mercado) with a high density of minimally sampled localities, and yet, has escaped detection by field workers. If a cryptic species of bird could be missed in the most heavily sampled 30% of the cerrado region, then the potential for overlooked biodiversity in the remaining under-sampled areas must be great. Our recognition of Suiriri islerorum as a cryptic species was initially based on an appreciation of vocal differences within Suiriri over a broad geographic range. It is critical that field personnel conducting surveys of the cerrado and other endangered habitats have access to adequate tape recording equipment and be proficient in the recognition of bird voices, or more taxa inevitably will be undersampled or overlooked (Parker 1991).

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LITERATURE CITED

- BATES, J. M., T. A. PARKER III, A. P. CAPPARELLA, AND T. J. DAVIS. 1992. Observations on the campo, cerrado and forest avifaunas of eastern Dpto. Santa Cruz, Bolivia, including 21 species new to the country. Bulletin of the British Ornithologists' Club 112:86–98.
- EITEN, G. 1972. The cerrado vegetation of Brazil. Botanical Review 38:201–341.
- FARABAUGH, S. M. 1982. The ecological and social significance of duetting. Pages 85–124 in Acoustic Communication in Birds (D. E. Kroodsma and E. H. Miller, Eds.) vol. 2. Academic Press, New York.
- HAYES, F. E. 2001. Geographical variation, hybridization and the leapfrog pattern of evolution in the Suiriri Flycatcher (*Suiriri suiriri*) complex of South America. Auk 118: in press.
- HELLMAYR, C. E. 1927. Catalogue of birds of the Americas, part 5. Tyrannidae. Field Museum of Natural History Zoological Series 13.
- ISLER, M. L. 1997. A sector-based ornithological geographic information system for the Neotropics. Pages 345–354 *in* Studies in Neotropical Ornithology Honoring Ted Parker (J. V. Remsen, Jr., Ed.). Ornithological Monographs no. 48.
- ISLER, M. L., AND P. R. ISLER. 1987. The Tanagers: Natural History, Distribution and Identification. Smithsonian Institution Press, Washington, D. C.
- ISLER, M. L., P. R. ISLER, AND B. M. WHITNEY. 1997. Biogeography and systematics of the *Thamnophilus punctatus* (Thamnophilidae) complex. Pages 355–381 *in* Studies in Neotropical Ornithology Honoring Ted Parker (J. V. Remsen, Jr., Ed.). Ornithological Monographs no. 48.
- ISLER, M. L., P. R. ISLER, AND B. M. WHITNEY. 1998. Use of vocalizations to establish species limits in antbirds (Passeriformes: Thamnophilidae). Auk 115:577–590.
- ISLER, M. L., P. R. ISLER, AND B. M. WHITNEY. 1999. Species limits in antbirds (Passeriformes: Thamnophilidae): The Myrmotherula surinamensis complex. Auk 116:83–96.
- KRABBE, N., AND T. S. SCHULENBERG. 1997. Species limits and natural history of *Scytalopus* tapacu-

los (Rhinocryptidae), with descriptions of the Ecuadorian taxa, including three new species. Pages 47–88 *in* Studies in Neotropical Ornithology Honoring Ted Parker (J. V. Remsen, Jr., Ed.). Ornithological Monographs no. 48.

- KROODSMA, D. E. 1984. Songs of the Alder Flycatcher (*Empidonax alnorum*) and Willow Flycatcher (*Empidonax traillii*) are innate. Auk 101:13–24.
- KROODSMA, D. E. 1986. Design of song playback experiments. Auk 103:640-642.
- KROODSMA, D. E. 1989. Male Eastern Phoebes (Sayornis phoebe, Tyrannidae, Passeriformes) fail to imitate songs. Journal of Comparative Psychology 103:227–232.
- KROODSMA, D. E., AND M. KONISHI. 1991. A suboscine bird (Eastern Phoebe, *Sayornis phoebe*) develops normal song without auditory feedback. Animal Behaviour 42:477–487.
- LANYON, W. E. 1978. Revision of the Myiarchus flycatchers. Bulletin of the American Museum of Natural History 161:429–627.
- MARR, T. G. 1981. Breeding and foraging ecology of the Cactus Wren in a variable environment. Ph.D. dissertation, New Mexico State University, Las Cruces.
- MCKITRICK, M. C., AND R. M. ZINK. 1988. Species concepts in ornithology. Condor 90:1–14.
- MEYER DE SCHAUENSEE, R. 1966. The Species of Birds of South America. Livingston, Wynnewood, Pennsylvania.
- PARKER, T. A. III. 1991. On the use of tape recorders in avifaunal surveys. Auk 108:443–444.
- PARKER, T. A. III, AND E. O. WILLIS. 1997. Notes on three tiny grassland flycatchers, with comments on the disappearance of South American fire-diversified savannas. Pages 549–555 *in* Studies in Neotropical Ornithology Honoring Ted Parker (J. V. Remsen, Jr., Ed.). Ornithological Monographs no. 48.
- PAYNTER, R. A., JR., AND M. A. TRAYLOR, JR. 1991. Ornithological Gazetteer of Brazil. Museum of Comparative Zoology, Cambridge, Massachusetts.
- RIDGELY, R. S., AND G. TUDOR. 1994. The Birds of South America, vol. 2. University of Texas Press, Austin.
- SHORT, L. L. 1975. A zoogeographic analysis of the South American Chaco avifauna. Bulletin of the American Museum of Natural History 154:163– 352.
- SIBLEY, C. G., AND B. L. MONROE, JR. 1990. Distribution and Taxonomy of Birds of the World. Yale University Press, New Haven, Connecticut.
- SICK, H. 1993. Birds in Brazil: A Natural History. Princeton University Press, Princeton, New Jersey.
- SILVA, J. M. C. 1995. Avian inventory of the cerrado region, South America: Implications for biolog-

ical conservation. Bird Conservation International. 5:291–304.

- SMITHE, F. B. 1975. Naturalist's Color Guide. American Museum of Natural History, New York.
- STOTZ, D. F., J. W. FITZPATRICK, T. A. PARKER III, AND D. K. MOSKOVITS. 1996. Neotropical Birds: Ecology and Conservation. University of Chicago Press, Chicago.
- TRAYLOR, M. A., JR. 1979. Tyrannidae. Pages 1–229 in Checklist of the Birds of the World, vol. 8 (M. A. Traylor, Jr., Ed.). Museum of Comparative Zoology, Cambridge, Massachusetts.
- TRAYLOR, M. A., JR. 1982. Notes on tyrant flycatchers (Aves: Tyrannidae). Fieldiana Zoology 13:1–22.

- WALSBERG, G. E. 1977. Ecology and energetics of contrasting social systems in *Phainopepla nitens* (Aves: Ptilognatidae). University of California Publications in Zoology, no. 108.
- ZIMMER, J. T. 1955. Further notes on tyrant flycatchers (Tyrannidae). American Museum Novitates, no. 1749.
- ZIMMER, K. J. 1993. Spatial and temporal variation in the breeding and foraging ecology of Blackthroated Sparrows. Ph.D. dissertation, New Mexico State University, Las Cruces.

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