

GEOGRAPHIC VARIATION, HYBRIDIZATION, AND THE LEAPFROG PATTERN OF EVOLUTION IN THE SUIRIRI FLYCATCHER (*SUIRIRI SUIRIRI*) COMPLEX

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ABSTRACT.—The Suiriri Flycatcher (*Suiriri suiriri*) of South America is represented by three distinct forms occurring in parapatry: (1) *S. s. suiriri* to the southwest in the Chaco/Pampas; (2) *S. s. affinis* located centrally in the Cerrado/southern Amazonia; and (3) *S. s. bahiae* to the northeast in the Caatinga. On the basis of an analysis of 366 specimens of *S. suiriri*, I found meager evidence for long-distance migration, little support for Bergmann's rule, and more support for Gloger's rule. I postulate that an ancestral population of *S. suiriri* split into three isolated populations, with the central population differentiating most rapidly into *affinis*, thus explaining the leapfrog pattern of greater similarity between peripheral *suiriri* and *bahiae*. After secondary contact, *affinis* freely hybridized with nominate *suiriri* in a hybrid zone to the southwest, where specimens demonstrate morphometric intermediacy and increased plumage variability; the rarity of parental phenotypes within the hybrid zone suggests that the two forms are conspecific according to the biological species concept. In the northeast, *affinis* may have hybridized with a remnant population of *suiriri*, possibly represented by poorly known *bahiae*. The intermediate size and increased plumage variability of *bahiae* resemble that of *suiriri* × *affinis* hybrids, supporting a hypothesis of hybrid origin for *bahiae*, but alternative hypotheses cannot be ruled out. This hypothesis of differentiation is supported by the concordant patterns of disjunction among several pairs of sister taxa of bird species that occur in the Chaco and Caatinga, with no intervening populations in the Cerrado, implying a shared historical process of vicariance. Genetic and behavioral studies are needed to elucidate further the status and history of differentiation within *S. suiriri*. Received 31 January 2000, accepted 13 December 2000.

EVOLUTIONARY BIOLOGISTS have long recognized the importance of documenting geographic variation in organisms (e.g. Mayr 1963, 1970; Gould and Johnston 1972, Zink and Remsen 1986). The data derived from such studies are crucial for testing hypotheses of phylogenetic relationships and speciation processes among sister taxa. Analyses of the nature of contact zones between sister taxa are important for evaluating the extent of gene flow and the development of isolating mechanisms between differentiating populations (e.g. Remington 1968, Short 1969, Woodruff 1973, Schueler and Rising 1976, Moore 1977, Barton and Hewitt 1985a, b, Harrison 1990). Where zones of phenotypic intermediacy occur between sister taxa, it is particularly important to distinguish between primary intergradation and secondary intergradation. Hybridization, defined as "in-

terbreeding between populations in secondary contact" (Sibley and Short 1964:148), is a genetic phenomenon that is widespread in birds (Grant and Grant 1992) and can be inferred phenotypically. Schueler and Rising (1976:284) provided evidence that "an increase in variability and intermediacy in concert constitute the only phenetic evidence for hybridization."

The Suiriri Flycatcher (*Suiriri suiriri*), a medium-sized species of the avian family Tyrannidae, is widely distributed to the east of the Andes in South America (Short 1975, Ridgely and Tudor 1994). As with many Neotropical birds, little is known about its natural history (e.g. Sick 1984, Belton 1985, Ridgely and Tudor 1994, Zimmer et al. 2001). It is an uncommon resident of relatively dry, open forest and forest edges, usually occurring alone or in pairs. As with most flycatchers, the sexes are monochromatic. Although altitudinal migration apparently occurs (Chesser 1997), it is not known to be a long-distance latitudinal migrant (Zimmer 1955). The species is represented by three distinct races: (1) nominate *S. s. suiriri* of southern

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Bolivia, southern Brazil, Paraguay, Uruguay, and northern Argentina; (2) *S. s. affinis* of southern Surinam, central and eastern Brazil, and eastern Bolivia; and (3) *S. s. bahiae* in a small area of the Caatinga in eastern Brazil. Thus far there have been no attempts at rigorously examining morphological and geographic variation within the species.

The purposes of this study are to evaluate the relationships between the three forms of *S. suiriri* by examining (1) geographic variation of morphometric and plumage characters, (2) sexual dimorphism, (3) the character and extent of hybridization between forms, and (4) the strength of correlation between mensural and environmental variables. The results of these analyses are further used to (1) evaluate quantitatively Bergmann's rule, which predicts that body size is inversely correlated with temperature and humidity (James 1970, Zink and Remsen 1986); (2) evaluate qualitatively Gloger's rule, which predicts that populations in more humid areas are more heavily pigmented than those in drier areas (Zink and Remsen 1986); and (3) infer the evolutionary history of the three forms.

TAXONOMIC BACKGROUND

In an early study of the taxonomic status of *S. suiriri*, Cory and Hellmayr (1927) recognized nominate *suiriri* and *affinis* as distinct species, and considered *bahiae* as a subspecies of *affinis*. The two "species" appeared to be allopatric until Laubmann (1940) reported five presumed hybrid specimens of *suiriri* × *affinis* from Departamento (hereafter Dpto.) Concepción, northeastern Paraguay, and two specimens from the same area that appeared to represent typical *affinis*. Zimmer (1955) subsequently examined a large series of *suiriri* at the American Museum of Natural History (AMNH) and reported 17 *suiriri* × *affinis* hybrids from the same area in northeastern Paraguay, plus another from Campanário, Mato Grosso do Sul, Brazil. Because of the variable and intermediate characteristics of the population in the zone of intergradation, Zimmer (1955) considered the two forms conspecific. Short (1975), however, failed to find the AMNH hybrid specimens and recognized *suiriri* and *affinis* as distinct species. Traylor (1982) relocated the AMNH hybrid specimens from northeastern Paraguay and

Campanário, and reported them to be as described by Zimmer (1955). Traylor (1979, 1982) concurred with Zimmer (1955) in recognizing *suiriri*, *affinis*, and *bahiae* as three races of a polytypic species. Nevertheless, subsequent authorities differed in their taxonomic treatment of *S. suiriri*. Remsen and Ridgely (1980) and Sibley and Monroe (1990) recognized two species. Remsen and Traylor (1983, 1989), Ridgely and Tudor (1994), and Hayes (1995) recognized a single species.

The southern race, nominate *suiriri*, has upperparts ranging from dark gray to dark olive, a whitish belly, a dark, pale-tipped tail, and a relatively short and black bill. The northern race, *affinis*, differs markedly from *suiriri* by having a bright yellow belly, paler gray or olive upperparts contrasting with a whitish or yellowish rump extending onto the rectrices, a longer bill that is often partially pale, and overall larger size. The two races are illustrated in Ridgely and Tudor (1994:plate 31). Unfortunately the behavior and ecology of those two races have not been studied in detail. Although Sick (1984) described their songs as being markedly different and suggested that they were separate species, Zimmer et al. (2001) provided evidence that their vocalizations were similar and that Sick's description of *affinis* was based on observations of an unrecognized cryptic species (see below). The poorly known northeastern race, *bahiae*, restricted to the Caatinga of Brazil, has grayish upperparts including a dark rump (as in *suiriri*), a belly color allegedly varying from whitish to bright yellow, and is intermediate in size between *suiriri* and *affinis*. Its vocalizations are apparently similar to those of *suiriri* and *affinis* (Zimmer et al. 2001).

Among a series of *affinis* specimens at the AMNH, Zimmer (1955) noted that five were remarkably short-billed with an unusually wide, pale terminal band on the rectrices. Enigmatically, those specimens were obtained from localities in central Brazil where typical *affinis* were also taken. Traylor (1982) further noted that those five specimens and a sixth in the Field Museum of Natural History (FMNH), initially described by Hellmayr (1929), possessed distinctly broader central rectrices lacking the pale edges of both *suiriri* and *affinis*, and a more gradual transition from the pale-gray crown to the pale-olive back than in typical *affinis*. Tray-

lor (1982) and Ridgely and Tudor (1994) speculated that the short-billed specimens represented an undescribed sibling species. Zimmer et al. (2001) provided morphological, vocal, and behavioral evidence that the short-billed form was sufficiently distinct from other *Suiriri* taxa under any of the widely accepted species concepts (McKittrick and Zink 1988) to warrant recognition of a new species, the Chapada Flycatcher (*S. islerorum*).

Although Zimmer (1955) gave the range of measurements for bill length (from base) in *suiriri* and *affinis* (including short-billed *affinis*), no measurements of *bahiae* and the intermediate populations have been published. Because of the larger size of northern *affinis*, Short (1975) considered the genus to be an exception to Bergmann's rule. However, there have been no quantitative analyses of morphometric and plumage variation within the species.

METHODS

I examined and measured 366 study skins of adult *S. suiriri* (specimens with evidence of juvenal plumage—speckled feathers on upperparts—were excluded; Wetmore 1926) in American museums (see Acknowledgments). These included 298 specimens of *suiriri*, 44 specimens of *affinis*, 4 specimens of *bahiae*, and 20 specimens of presumed hybrid *suiriri* × *affinis* (all with intermediate and variable characters, and taken from the zone of contact between the two parental phenotypes). Additional data on *bahiae* were obtained from Brazilian museums (E. Willis pers. comm. and published literature) and from field observations by Zimmer et al. (2001) and B. Whitney (pers. comm.).

Geographic distribution.—The locality for each specimen was taken from the specimen label and its longitude, latitude, and elevation were obtained (when available) from ornithological gazetteers for each country (Paynter 1985, 1989, 1992; Paynter and Traylor 1991) or from the specimen label. Each locality was plotted on a map.

Seasonal distribution.—Evidence for long-distance migration, particularly for the southern race *suiriri*, would complicate an analysis of geographic variation. To examine the seasonal distribution of *S. suiriri*, the locality for each specimen (as described above) and date of collection were taken from the specimen label. A bivariate plot of latitude and month of collection was made for all specimens. An absence of specimens from the southern latitudes and a concentration of specimens at northern latitudes during the austral winter (June–August) would provide evidence for long-distance migration.

Morphometric variation.—Using digital calipers, I measured (nearest 0.1 mm) the following mensural variables: bill length (BL), from nostril to tip of maxilla; wing chord length (WL), from bend of folded wing to tip of longest primary feather; and tarsus length (TS), from junction of tibiotarsus and tarsometatarsus to distal junction of hind toe and tarsometatarsus. Tail length (TL), from base of tail to tip of longest rectrix, was measured (nearest millimeter) with a blunt wooden ruler to minimize damage to the specimens. I did not attempt to evaluate measurement error, which undoubtedly contributed to the variation in the data.

I used those data to compute four dimensionless (scale-free) shape variables. These included bill length/wing length (BL/WL), tarsus length/wing length (TS/WL), and tail length/wing length (TL/WL). Those variables were used to evaluate relative shapes, but because ratios are nonlinear, often introducing spurious correlations (Atchley et al. 1976), they were not subjected to statistical analyses.

For each specimen, I also recorded the sex, locality, date, and mass (MS; nearest 0.1 g) when available, from the attached specimen labels. The sex was not identified in 15 specimens of *suiriri*, 6 of *affinis*, and 2 of *suiriri* × *affinis*; none of those specimens was used in the morphometric analyses described below.

Two-sample (Student's) *t*-tests (Sokal and Rohlf 1981) were used to compare the means of each mensural variable between the sexes for *suiriri*, *affinis*, and Paraguayan *suiriri* × *affinis* hybrids. One-way analyses of variance (Sokal and Rohlf 1981) were used to compare the means of each mensural variable between *suiriri*, *affinis*, and the Paraguayan *suiriri* × *affinis* hybrids; *a posteriori* multiple comparison tests were computed using *t*-tests (*t* statistic) with Bonferroni adjustments of the alpha level (Lentner and Bishop 1986). I did not attempt to compare statistically variables for specimens of *bahiae* and hybrids from Bolivia and Brazil due to the small sample sizes.

A principal components (PC) analysis (Sokal and Rohlf 1981) was computed using the correlation matrix of raw data for the four mensural variables (BL, WL, TS, TL) to produce individual PC loadings for all 366 specimens of *S. suiriri* and 11 specimens of *S. islerorum*. PC1 and PC2, loosely interpreted as size and shape axes (e.g. Rising and Somers 1989), were plotted to compare multivariate trends among *Suiriri* taxa. All statistical analyses were computed with Statistix 3.1 software (Anonymous 1990).

Plumage variation.—I used a simple "hybrid index" to score three plumage characters for all specimens of *S. suiriri*. I initially used a five-score hybrid index, but found it easier to place specimens into a three-score hybrid index. Although some criticize the use of a hybrid index as crude and subjective, independent studies obtain essentially identical results (Corbin and Barrowclough 1977). Back coloration was

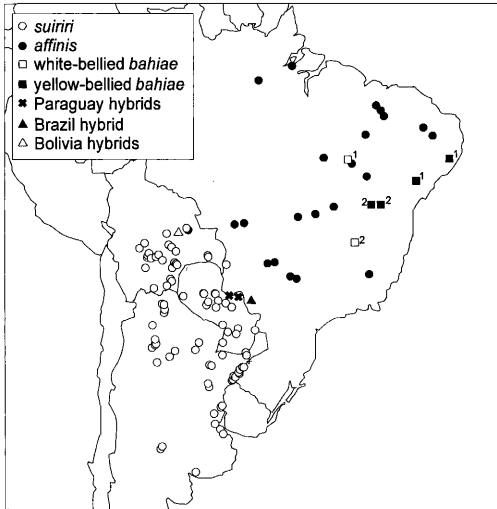


FIG. 1. Distribution of *Suiriri suiriri* specimens, including *S. s. suiriri* × *S. s. affinis* hybrids, examined in this study. For *S. suiriri bahiae*, localities indicated with numeral 1 refer to specimens examined during this study; localities indicated with numeral 2 refer to published specimen records and recent sight records.

scored as 0 if dark grayish or olive as in typical *suiriri*, 2 if light grayish or olive as in typical *affinis*, and 1 if intermediate between the two taxa. Rump color was scored as 0 if dark as in typical *suiriri*, 2 if light as in typical *affinis*, and 1 if intermediate between the two taxa. Belly color was scored as 0 if whitish as in typical *suiriri*, 1 if light yellow, and 2 if bright yellow as in typical *affinis*. The three scores were summed as a measure of plumage variability (0 for typical *suiriri*, 6 for typical *affinis*, and 1–5 for intermediate between the two taxa).

Geographic variation.—To assess geographic variation in morphological traits, I computed Pearson correlation coefficients (r ; Sokal and Rohlf 1981) for each mensural variable with latitude, longitude, and elevation. This was done for each sex of all *S. suiriri* combined and separately for *suiriri* and *affinis*. Because temperature is correlated with both latitude and elevation, a significantly positive correlation between mensural variables and either latitude or elevation would provide support for Bergmann's rule.

RESULTS

Geographic distribution.—The three races of *S. suiriri* are parapatrically distributed, with the range of each species roughly coinciding with well known biogeographic regions (e.g. Short 1975): nominate *suiriri* occurs primarily in the

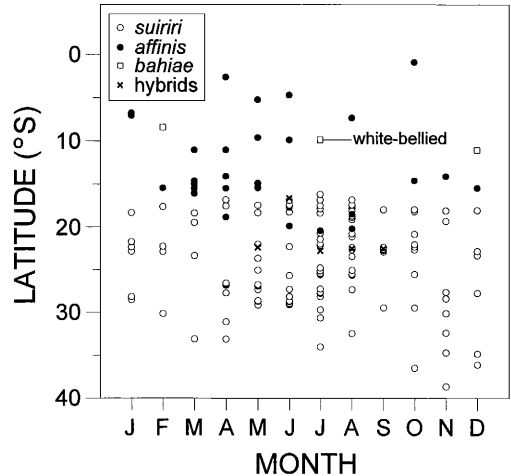


FIG. 2. Seasonal variation in latitudinal distribution of *Suiriri suiriri* specimens, including *S. s. suiriri* × *S. s. affinis* hybrids, examined in this study.

Chaco and Pampas, *affinis* in the Cerrado and southern Amazonia, and *bahiae* in the Caatinga (Fig. 1). The ranges of *suiriri* and *affinis* meet between the Chaco and Cerrado in eastern Bolivia, northeastern Paraguay and southwestern Brazil, where hybridization apparently occurs but is well documented only in Paraguay. The ranges of *affinis* and *bahiae* meet between the Cerrado and Caatinga, where hybridization may occur, but is poorly documented.

Seasonal distribution.—Although short-distance altitudinal migration apparently occurs in nominate *suiriri*, at least in Bolivia (Chesser 1997), there is little evidence for long-distance latitudinal migration (Fig. 2). Specimen records from Argentinian and Uruguayan museums indicate that the southernmost populations of nominate *suiriri* remain present throughout the year (L. Joseph unpubl. data).

Morphometric variation.—In nominate *suiriri*, sexual dimorphism occurred in all size variables, with males averaging significantly larger (Table 1). In the considerably smaller sample of *affinis* specimens, females also averaged smaller for each measure of body size (except mass, for which there was insufficient data), but did not differ significantly for BL (Table 1). In both *suiriri* and *affinis*, TL/WL averaged slightly higher for females than for males, suggesting that females had relatively shorter WL compared to TL, but no other shape variables differed appreciably between sexes for either tax-

TABLE 1. Descriptive measures of size and shape variables (BL = bill length; WL = wing length; TS = tarsus length; TL = tail length; PC1 = principal component 1; PC2 = principal component 2) for three races of *S. suiriri*, with statistical comparisons between sexes and taxa for *suiriri* and *affinis*.

Variable	<i>suiriri</i>										<i>affinis</i>										<i>bahiae</i>			
	<i>suiriri</i>					<i>affinis</i>					<i>Yellow-bellied</i>					<i>White-bellied</i>								
	\bar{x}	SD	Min,Max	<i>n</i>	\bar{x}	SD	Min,Max	<i>n</i>	\bar{x}	SD	Min,Max	<i>n</i>	\bar{x}	SD	Min,Max	<i>n</i>	\bar{x}	SD	Min,Max	<i>n</i>				
BL	♂ 7.79	0.35	6.8,9.0	158	9.37 ^c	0.37	8.7,10.1	15	9.2	0.37	8.7,10.1	1	9.5	0.37	8.7,10.1	1	9.5	0.37	8.7,10.1	1				
	♀ 7.53 ^a	0.34	6.8,8.7	122	9.19 ^c	0.46	7.3,10.5	22	7.9	0.46	7.3,10.5	1	9.0	0.46	7.3,10.5	1	9.0	0.46	7.3,10.5	1				
WL	♂ 73.68	2.86	66.5,82.7	161	84.77 ^c	2.69	79.6,88.7	16	74.2	2.69	79.6,88.7	1	78.4	2.69	79.6,88.7	1	78.4	2.69	79.6,88.7	1				
	♀ 71.00 ^a	2.70	64.6,79.3	122	79.28 ^{a,c}	3.74	69.9,87.8	22	72.8	3.74	69.9,87.8	1	74.2	3.74	69.9,87.8	1	74.2	3.74	69.9,87.8	1				
TS	♂ 19.47	0.75	17.6,21.7	161	20.79 ^c	0.79	19.7,22.8	15	19.6	0.79	19.7,22.8	1	20.0	0.79	19.7,22.8	1	20.0	0.79	19.7,22.8	1				
	♀ 18.88 ^a	0.74	16.9,20.5	122	19.46 ^{a,e}	0.95	17.5,21.1	22	18.9	0.95	17.5,21.1	1	19.0	0.95	17.5,21.1	1	19.0	0.95	17.5,21.1	1				
TL	♂ 69.82	3.58	57.0,78.0	160	73.20 ^c	2.21	69.0,76.0	15	65.0	2.21	69.0,76.0	1	73.0	2.21	69.0,76.0	1	73.0	2.21	69.0,76.0	1				
	♀ 68.26 ^a	3.45	58.0,79.0	120	70.45 ^{b,d}	2.81	65.0,76.0	22	68.0	2.81	65.0,76.0	1	68.0	2.81	65.0,76.0	1	68.0	2.81	65.0,76.0	1				
MS	♂ 15.29	1.78	12.0,17.5	20	20.00 ^f	—	20.0,20.0	1	—	—	20.0,20.0	0	—	—	20.0,20.0	0	—	—	20.0,20.0	0				
	♀ 13.80 ^b	1.16	12.0,15.7	14	—	—	—	0	—	—	—	0	—	—	—	0	—	—	—	0				
BL/WL	♂ 0.11	0.01	0.09,0.12	158	0.11	0.01	0.09,0.12	15	0.12	0.01	0.09,0.12	1	0.12	0.01	0.09,0.12	1	0.12	0.01	0.09,0.12	1				
	♀ 0.11	0.01	0.09,0.12	122	0.12	0.01	0.09,0.14	22	0.11	0.01	0.09,0.14	1	0.12	0.01	0.09,0.14	1	0.12	0.01	0.09,0.14	1				
TS/WL	♂ 0.26	0.01	0.23,0.29	161	0.25	0.01	0.22,0.28	15	0.26	0.01	0.22,0.28	1	0.26	0.01	0.22,0.28	1	0.26	0.01	0.22,0.28	1				
	♀ 0.27	0.01	0.24,0.30	122	0.25	0.01	0.21,0.27	22	0.26	0.01	0.21,0.27	1	0.26	0.01	0.21,0.27	1	0.26	0.01	0.21,0.27	1				
TL/WL	♂ 0.95	0.04	0.75,1.04	160	0.87	0.02	0.53,0.92	15	0.88	0.02	0.53,0.92	1	0.93	0.02	0.53,0.92	1	0.93	0.02	0.53,0.92	1				
	♀ 0.96	0.03	0.87,1.03	120	0.89	0.03	0.83,1.01	22	0.93	0.03	0.83,1.01	1	0.92	0.03	0.83,1.01	1	0.92	0.03	0.83,1.01	1				
PC1	♂ 0.08	0.97	-2.62,2.41	157	-3.27	1.05	-4.84,-0.76	16	-0.54	1.05	-4.84,-0.76	1	-2.44	1.05	-4.84,-0.76	1	-2.44	1.05	-4.84,-0.76	1				
	♀ 1.08 ^a	0.97	-1.42,3.18	120	-1.83 ^{a,c}	0.99	-4.31,-0.07	29	0.60	0.99	-4.31,-0.07	1	-0.45	0.99	-4.31,-0.07	1	-0.45	0.99	-4.31,-0.07	1				
PC2	♂ 0.02	0.86	-2.99,1.98	157	-0.51 ^e	1.07	-1.90,1.95	16	-1.75	1.07	-1.90,1.95	1	-0.47	1.07	-1.90,1.95	1	-0.47	1.07	-1.90,1.95	1				
	♀ 0.14	0.76	-2.49,2.55	120	-0.12	1.10	-2.15,2.57	29	-0.08	1.10	-2.15,2.57	1	-0.69	1.10	-2.15,2.57	1	-0.69	1.10	-2.15,2.57	1				

^a Differs from males of same race, $P < 0.001$.

^b Differs from males of same race, $P < 0.01$.

^c Differs from *suiriri* of same sex, $P < 0.01$.

^d Differs from *suiriri* of same sex, $P < 0.001$.

^e Differs from *suiriri* of same sex, $P < 0.01$.

^f Masses of 22.7, 19.0, 21.5, and 22.5 g were reported for unsexed *affinis* (Fry 1970, Marini et al. 1997).

TABLE 2. Descriptive measures of size and shape variables (see Table 1 for definitions) for three hybrid populations of *Suiriri s. suiriri* × *affinis*. Statistical comparisons are given between the Paraguay hybrids and *suiriri* and *affinis* for each sex. No significant sexual dimorphism was found in the Paraguay hybrid population.

Variable		Paraguay				Bolivia				Brazil	
		\bar{x}	SD	Min,Max	<i>n</i>	\bar{x}	SD	Min,Max	<i>n</i>	\bar{x}	<i>n</i>
BL	♂	8.77 ^{a,c}	0.24	8.4,9.1	9	7.80	0.28	7.6,8.0	2	9.40	1
	♀	8.82 ^a	0.32	8.4,9.2	5	—	—	—	0	—	0
WL	♂	80.01 ^{a,c}	0.32	76.0,84.7	9	76.15	2.19	74.6,77.7	2	85.10	1
	♀	77.95 ^a	0.18	74.7,79.8	6	—	—	—	0	—	0
TS	♂	20.21 ^b	0.72	18.9,21.2	9	18.2	0.14	18.1,18.3	2	19.00	1
	♀	19.83 ^b	0.65	19.2,21.0	6	—	—	—	0	—	0
TL	♂	70.78 ^d	3.07	65.0,75.0	9	68.0	1.41	67.0,69.0	2	78.00	1
	♀	72.83 ^b	4.79	69.0,79.0	6	—	—	—	0	—	0
BL/WL	♂	0.11	0.004	0.10,0.12	9	0.10	0.00	0.10,0.10	2	0.11	1
	♀	0.11	0.004	0.11,0.12	5	—	—	—	0	—	0
TS/WL	♂	0.25	0.01	0.24,0.26	9	0.24	0.01	0.24,0.24	2	0.22	1
	♀	0.25	0.01	0.25,0.27	6	—	—	—	0	—	0
TL/WL	♂	0.89	0.05	0.81,0.96	9	0.89	0.04	0.86,0.92	2	0.92	1
	♀	0.93	0.06	0.88,1.02	6	—	—	—	0	—	0
PC1	♂	-1.95 ^a	0.95	-3.30,-0.66	9	0.59	0.39	0.31,0.87	2	-3.33	1
	♀	-1.81 ^a	0.82	-2.96,-0.94	5	—	—	—	0	—	0
PC2	♂	-0.60	0.54	-1.67,0.14	9	0.47	0.47	0.14,0.80	2	1.32	1
	♀	0.05	1.13	-1.07,1.44	5	—	—	—	0	—	0

^a Differs from *suiriri* of same sex, $P < 0.001$.

^b Differs from *suiriri* of same sex, $P < 0.01$.

^c Differs from *affinis* of same sex, $P < 0.001$.

^d Differs from *affinis* of same sex, $P < 0.05$.

on (Table 1). Females of *bahiae* likewise averaged smaller than males for each size variable (except mass, for which there was no data) and had a larger value for TL/WL (Table 1), but the data were insufficient for statistical comparisons.

Both sexes of *affinis* averaged significantly higher for each size variable (except mass, for which there was insufficient data) than *suiriri* (Table 1). The higher TS/WL and TL/WL for *suiriri* suggested that WL is relatively shorter for *suiriri* than for *affinis*. In the small sample of *bahiae*, the means of BL were similar to those of *affinis*, WL and TS averaged slightly longer than *suiriri*, TL averaged slightly shorter than *suiriri*, and TL/WL was intermediate (Table 1).

Hybrid *suiriri* × *affinis* from Paraguay showed no significant sexual dimorphism for any size or shape variable, but the sample sizes were small (Table 2). Although the hybrids tended to be intermediate in size between *suiriri* and *affinis*, the nature of variation was complex. For males, BL and WL were intermediate between *suiriri* and *affinis*, differing significantly from both; TS averaged significantly longer than *suiriri* and approached the mean for *affinis*; and TL was significantly shorter than

affinis and approached the mean for *suiriri* (Table 2). The female hybrids differed significantly from *suiriri*, but not from *affinis* for all four size variables; WL was intermediate, though closer to *affinis*, whereas BL, TS, and TL averaged the same or even higher than *affinis* (Table 2). For the three shape variables, males appeared to differ from *suiriri* for TS/WL and TL/WL, whereas females appeared to differ from *suiriri* only for BL/WL; neither sex differed from *affinis* for any shape variable. The two Bolivian hybrids resembled *suiriri* in size variables and *affinis* in shape variables; the Brazilian hybrid resembled *affinis* in BL, WL, and TL, and *suiriri* in TS and TS/WL.

A bivariate plot (Fig. 3) of PC1 (59.7% of variance) and PC2 (19.4% of variance) separated most *suiriri* and *affinis* specimens. The *bahiae* specimens appeared to be intermediate between *suiriri* and *affinis*. The male *suiriri* × *affinis* hybrids from Paraguay and Brazil appeared intermediate between *suiriri* and *affinis*, but the two males from Bolivia clustered within the range of variation of *suiriri*. In contrast, the female *suiriri* × *affinis*, all of which were from Paraguay, clustered within the range of variation of *affinis*. The widely scattered speci-

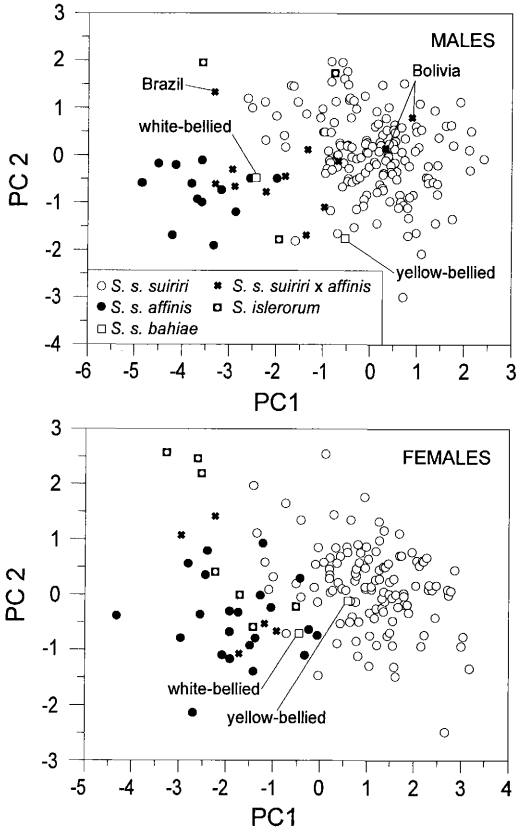


FIG. 3. Principal components analysis of morphological variables for *Suiriri suiriri* and *S. islerorum* specimens examined in this study.

mens of *S. islerorum* tended to cluster more with *affinis* than *suiriri*.

Plumage variation.—The total plumage score was 0 for all but two specimens of nominate *suiriri*, and 6 for all but two specimens of *affinis* (Table 3). Intermediate belly color occurred in a specimen of *suiriri* from Tucumán, Argentina

(AMNH 499741), another specimen of *suiriri* from Yuto, Jujuy, Argentina (Museum of Comparative Zoology; MCZ 262238), and in a female specimen of *affinis* from Chapada, Mato Grosso, Brazil (AMNH 33101); a specimen of unknown sex from Miranda, Mato Grosso do Sul, Brazil (MCZ 154623), had a nearly-white belly within the normal range of variation of *suiriri*. None of those specimens showed other indications of hybridization. Wetmore (1924, 1926) described an additional yellow-bellied specimen (not examined by me) from Tucumán, Argentina, as a new species (*S. improvisa*), but Cory and Hellmayr (1927:443) pointed out that other specimens from the type locality (e.g. AMNH 499741 described above) varied from the typical “white” of nominate *suiriri* to the yellow of *improvisa* and regarded the type specimen of the latter as a mutant *suiriri*.

The four *bahiae* specimens examined resembled *suiriri* in back and rump color, but had highly variable belly coloration: white in two specimens and yellow in the other two (Table 3, Appendix). The two white-bellied *bahiae* specimens, both taken from the same locality, were indistinguishable from *suiriri* on the basis of plumage, but BL of both specimens (male, 9.5 mm; female, 9.0 mm) exceeded the maximum BL of *suiriri* (9.0 and 8.7 mm for males and females, respectively; see Table 1). Furthermore, Zimmer (1955) pointed out that the outer web of the outer rectrix was dull as in *affinis* and *bahiae*, in contrast with the lighter outer web of *suiriri*. Another white-bellied specimen at the Museu de Zoologia da Universidade de São Paulo (MZUSP 8418), a male collected at Pirapora, Minas Gerais, in August 1912, was regarded as indistinguishable from *suiriri* and considered a migrant (Cory and Hellmayr 1927, Pinto and

TABLE 3. Number of individuals for each plumage score for each taxon or population of *Suiriri suiriri*.

Taxa/population	Back			Rump			Belly			Total score						
	0	1	2	0	1	2	0	1	2	0	1	2	3	4	5	6
<i>S. s. suiriri</i>	298	0	0	298	0	0	296	2	0	296	2	0	0	0	0	0
<i>S. s. affinis</i>	0	0	48	0	0	48	1	1	46	0	0	0	0	1	1	46
<i>S. s. suiriri</i> × <i>affinis</i>																
Bolivia	0	2	0	0	2	0	2	0	0	0	0	2	0	0	0	0
Paraguay combined	0	16	1	17	0	0	3	5	9	0	3	4	9	1	0	0
San Luis de la Sierra	0	9	1	9	1	0	2	1	7	0	2	0	7	1	0	0
Zanja Morotí	0	7	0	7	0	0	1	4	2	0	1	4	2	0	0	0
Brazil	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0
<i>S. s. bahiae</i>	4	0	0	4	0	0	2	1	1	2	1	1	0	0	0	0

Camargo 1961, Ridgely and Tudor 1994). Zimmer (1955) and Pinto and Camargo (1961) pointed out that a female (MZUSP 8415) collected from the same locality was assigned to *affinis* (identity reconfirmed by E. Willis, pers. comm.). Zimmer (1955), who did not examine the specimens, queried the identity of the white-bellied bird as *suiriri* and suggested it was a white-bellied *affinis*; however, the dark rump and back described by Pinto and Camargo (1961) are more characteristic of *bahiae* than *affinis*. The specimen was recently reexamined by E. Willis (pers. comm.), who reported BL to be 9.0 mm, the maximum for male *suiriri* (Table 1); other measurements (WL, 81.5 mm; TS, 20.4 mm; TL, 74.3 mm) were within the range of variation of male *suiriri* and *affinis*. Furthermore, Willis described the specimen's back as "rather olive but with rusty or brownish wash, . . . more like *affinis* than like the few *suiriri* in the collection." This specimen appears to represent a white-bellied *bahiae*.

Other *bahiae* specimens reported in the literature (but not examined by me) were apparently yellow-bellied, including the type specimen from "Bahia" in the Berlepsch collection (Cory and Hellmayr 1927). However, E. Willis (pers. comm.) reexamined the MZUSP specimens assigned to *bahiae* by Cory and Hellmayr (1927) and Pinto and Camargo (1961), and found that all specimens, including two from Juazeiro, Bahia (09°25'S, 40°30'W), two from Coremas, Paraíba (07°01'S, 37°58'W), and two from Ibipetuba (=Santa-Rita-de-Cassia), Bahia (11°00'S, 44°32'W), were all pale-rumped, apparently representing *affinis*. I found that two Los Angeles County Museum (LACM) specimens assigned to *bahiae*, also from Ibipetuba, Bahia, were also pale-rumped, representing *affinis*.

All recent records of *bahiae* were apparently of yellow-bellied birds. Those include observations by R. Ridgely (pers. comm.), Zimmer et al. (2001) near Lagoa Grande, Pernambuco, from 1996–1999, and B. Whitney (pers. comm.) at the following localities: 20 km south of Carinhanha, Minas Gerais (14°17'S, 43°47'W), on 11 November 1994 (one bird); 25 km east of Guanambi, Bahia (14°07'S, 42°37'W), on 12 November 1994 (four); and 15 km north of Petrolina, Pernambuco (09°24'S, 40°30'W), on 21 November 1994 (two).

Twenty specimens taken from the zone of contact between *suiriri* and *affinis* showed intermediate and variable plumage characters. The two hybrids from eastern Bolivia were intermediate in back and rump color, but belly color resembled *suiriri* (Table 3, Appendix). The 17 hybrids from two localities (in north-eastern Paraguay) were consistently dark-rumped (as in *suiriri*), intermediate in back coloration, and highly variable in belly coloration (Table 3, Appendix). The distribution of total plumage scores for the two Paraguayan localities did not differ significantly ($\chi^2 = 8.02$, $df = 4$, $P = 0.09$). Traylor (1982) reported two additional hybrid specimens (AMNH) from Belén, Dpto. Concepción, which is south of the other Paraguayan hybrid localities; however, I found the Belén specimens to be indistinguishable from *suiriri* (Hayes 1995). The single Brazilian hybrid specimen was intermediate in back coloration, but otherwise resembled *affinis* (Table 3, Appendix).

Geographic variation.—Significant geographic variation occurred for several mensural variables. Among all *S. suiriri* specimens combined, latitude was negatively correlated with BL, WL, TS, and TL, and positively correlated with MS (but only one *affinis* male in sample) and PC1 (Table 4). Longitude was negatively correlated with BL, WL, TS (males only), PC1, and PC2 (males only), and positively correlated with PC2 (females only; Table 4). Elevation was positively correlated with WL (females only), TL, and PC2, and negatively correlated with WL (males only, in contrast with females), MS (males only), and PC1 (Table 4).

Within nominate *suiriri*, latitude was positively correlated with MS and negatively correlated with TL (females only) and PC2 (females only; Table 4). Longitude was positively correlated with TL and PC2 (males only), and negatively correlated with MS (males only) and PC1 (females only; Table 4). Elevation was positively correlated with WL, TL and PC2, and negatively correlated with MS (males only) and PC1 (Table 4).

Sample sizes were limited within *affinis*, especially for males (Table 4). For males, elevation was positively correlated with TS; for females, latitude was positively correlated with WL and TL and negatively correlated with PC1, and longitude was positively correlated with TL (Table 4).

TABLE 4. Geographic correlates (*r*) of body size and shape variables (see Table 1 for definitions) in *S. suiriri*. Note that *S. suiriri* refers to all forms combined, including hybrids; sample sizes for *S. s. bahiae* and *S. s. suiriri* × *affinis* were inadequate for analysis. See Methods for definitions of variables.

Variable	Sex/taxon	Latitude and longitude			Elevation	
		<i>n</i>	Lat.	Long.	<i>n</i>	Elev.
BL	♂ <i>S. suiriri</i>	186	-0.47 ^a	-0.59 ^a	183	-0.05
	♂ <i>S. s. suiriri</i>	158	-0.03	-0.01	155	0.06
	♂ <i>S. s. affinis</i>	15	-0.11	-0.38	14	-0.31
	♀ <i>S. suiriri</i>	150	-0.59 ^a	-0.63 ^a	147	-0.08
	♀ <i>S. s. suiriri</i>	122	-0.02	-0.09	121	0.02
	♀ <i>S. s. affinis</i>	22	-0.25	0.25	20	-0.04
WL	♂ <i>S. suiriri</i>	190	-0.42 ^a	-0.45 ^a	187	-0.20 ^b
	♂ <i>S. s. suiriri</i>	161	-0.05	0.11	158	0.44 ^a
	♂ <i>S. s. affinis</i>	16	0.17	-0.10	15	0.05
	♀ <i>S. suiriri</i>	151	-0.46 ^a	-0.41 ^a	148	0.20 ^c
	♀ <i>S. s. suiriri</i>	122	-0.14	0.27 ^b	121	0.45 ^a
	♀ <i>S. s. affinis</i>	22	0.60 ^b	0.27	20	0.38
TS	♂ <i>S. suiriri</i>	189	-0.17 ^c	-0.31 ^a	186	0.00
	♂ <i>S. s. suiriri</i>	161	0.05	-0.02	158	0.04
	♂ <i>S. s. affinis</i>	15	0.36	-0.08	14	0.65 ^c
	♀ <i>S. suiriri</i>	151	-0.16 ^c	-0.11	148	0.07
	♀ <i>S. s. suiriri</i>	122	-0.04	0.17	121	0.13
	♀ <i>S. s. affinis</i>	22	0.24	0.03	20	-0.03
TL	♂ <i>S. suiriri</i>	188	-0.18 ^c	0.00	186	0.42 ^a
	♂ <i>S. s. suiriri</i>	160	-0.06	0.22 ^b	157	0.49 ^a
	♂ <i>S. s. affinis</i>	15	0.11	-0.20	15	0.17
	♀ <i>S. suiriri</i>	149	-0.23 ^a	-0.01	146	0.42 ^a
	♀ <i>S. s. suiriri</i>	120	-0.25 ^b	0.23 ^c	119	0.53 ^a
	♀ <i>S. s. affinis</i>	22	0.50 ^c	0.48 ^c	20	0.28
MS	♂ <i>S. suiriri</i>	21	0.46 ^c	-0.23	21	-0.60 ^b
	♂ <i>S. s. suiriri</i>	20	0.76 ^a	-0.47 ^c	20	-0.72 ^a
	♂ <i>S. s. affinis</i>	1	—	—	0	—
	♀ <i>S. suiriri</i>	14	0.75 ^b	-0.45	14	-0.44
	♀ <i>S. s. suiriri</i>	14	0.75 ^b	-0.45	14	-0.44
	♀ <i>S. s. affinis</i>	0	—	—	0	—
PC1	♂ <i>S. suiriri</i>	183	0.40 ^a	0.43 ^a	181	-0.18 ^c
	♂ <i>S. s. suiriri</i>	157	0.03	-0.13	154	-0.42 ^a
	♂ <i>S. s. affinis</i>	13	-0.23	0.15	13	-0.37
	♀ <i>S. suiriri</i>	148	0.49 ^a	0.42 ^a	145	-0.19 ^c
	♀ <i>S. s. suiriri</i>	120	0.17	-0.24 ^b	119	-0.43 ^a
	♀ <i>S. s. affinis</i>	22	-0.47 ^c	-0.38	20	-0.22
PC2	♂ <i>S. suiriri</i>	183	0.08	0.36 ^a	181	0.39 ^a
	♂ <i>S. s. suiriri</i>	157	-0.07	0.20 ^c	154	0.41 ^a
	♂ <i>S. s. affinis</i>	13	-0.31	-0.32	13	-0.45
	♀ <i>S. suiriri</i>	148	0.12	0.32 ^a	145	0.40 ^a
	♀ <i>S. s. suiriri</i>	120	-0.21 ^c	0.16	119	0.43 ^a
	♀ <i>S. s. affinis</i>	22	0.35	0.28	20	0.27

^a *P* < 0.001.

^b *P* < 0.01.

^c *P* < 0.05.

DISCUSSION

This study documents considerable geographic variation in morphometric and plumage traits within *S. suiriri*. Although it remains unclear whether such variation is attributable to natural selection, environmental induction, or stochasticity, the geographic patterns of variability for temperature and humidity are well

known within the range of *S. suiriri* (e.g. Hoffman 1975, Prohaska 1976), and an assessment of their potential effects on morphological variability is warranted (Zink and Remsen 1986).

Temperature is inversely correlated with both latitude and elevation. Because tropical *affinis* is clearly larger than more temperate *suiriri*, Short (1975) pointed out that *S. suiriri* violated Bergmann's rule. When all specimens

are combined, the negative correlation of most morphometric traits with latitude supports Short's (1975) conclusion. However, within the more southerly race *suiriri*, the positive correlation of MS with latitude supports Bergmann's rule, though the negative correlation of MS with elevation is puzzling. Although WL is often used as an index of body size for studies of geographic variation (Zink and Remsen 1986), MS is often considered to be a better measure of body size (e.g. Rising and Somers 1989, Freeman and Jackson 1990). In the case of *suiriri*, WL was significantly correlated with elevation as noted in Bolivian specimens by Traylor (1950), but not latitude. PC1, often used as a multivariate measure of body size (Rising and Somers 1989), was not correlated with latitude and was negatively correlated with elevation. The effects of temperature on morphological variation remain unclear, as it is with many North American species of birds (Zink and Remsen 1986).

The peripheral races *suiriri* and *bahiae* occur in drier regions than does *affinis*. Although *affinis* is generally paler dorsally (primarily on rump) than either *suiriri* or *bahiae*, the latter races are paler on the underparts and grayer on the upperparts, in general conformity with Gloger's rule, which is well supported among North American birds (Zink and Remsen 1986).

Several historical processes may be postulated to explain the geographic pattern of differentiation demonstrated by *S. suiriri*. First, differentiation may have evolved in parapatry, with current contact zones between adjacent races coinciding with relatively abrupt environmental changes (Endler 1982a, b). In that scenario, each contact zone would represent a "step cline" of primary intergradation where gene flow is reduced between contiguous populations that have never been isolated. Second, differentiation may have evolved in allopatry following long-distance dispersal of "founder" individuals across pre-existing barriers. And third, differentiation may have evolved in allopatry as a contiguous ancestral population became fragmented by vicariance. For both the second and third hypotheses, the current contact zones would represent secondary intergradation (i.e. hybridization) occurring where the expanding ranges of adjacent populations met.

The parapatric differentiation model is supported by the position of current contact zones

coinciding with the boundaries between major biogeographic regions (Chaco-Cerrado-Caatinga), which may be characterized by relatively abrupt environmental changes. However, the boundaries between those regions may also represent locations of previous vicariance events (e.g. Cracraft and Prum 1988). Furthermore, the morphological intermediacy and increased plumage variability of specimens from the contact zone between *suiriri* and *affinis* in north-eastern Paraguay provide convincing evidence for secondary intergradation (hybridization) rather than primary intergradation (Schueler and Rising 1976). The occurrence of hybridization effectively falsifies the parapatric model and is consistent with both the dispersal and vicariance models of allopatric differentiation.

Long-distance dispersal is unlikely to occur among relatively sedentary taxa, including *S. suiriri*, for which there is little evidence of long-distance migration. This suggests that the northeastern race *bahiae*, which resembles southern *suiriri* more than *affinis* on the basis of plumage scores, was unlikely to have been established by long-distance migrants of *suiriri* from southern South America.

Because the geographic range of *affinis* occurs between morphologically similar *suiriri* and *bahiae*, *S. suiriri* provides yet another example of the leapfrog pattern of geographic variation (Remsen 1984) in which two similar populations are separated from each other by one or more different, intervening populations of the same species. Remsen (1984) suggested several hypotheses that may explain such a pattern, including (1) convergent evolution in the phenotypically similar but geographically separated taxa; (2) more rapid, divergent evolution in the central, intervening taxa; (3) centrifugal speciation; (4) ancient corridors connecting the currently separated but phenotypically similar taxa; and (5) random phenotypic changes in geographically isolated populations of a taxon, with the changes occurring first—by chance—in the intervening population(s). The lack of concordance in the ranges of Andean bird taxa exhibiting the leapfrog pattern supports the fifth hypothesis, suggesting that phenotypic changes appeared randomly with respect to geography, and were not necessarily induced by the environment (Remsen 1984). Can this hypothesis explain the geographic pattern of differentiation in *S. suiriri*?

Many species of South American birds are represented by pairs of closely related taxa with disjunct populations in the Chaco and Caatinga, with essentially no intervening population in the Cerrado (except perhaps in the periphery; e.g. see distributional maps of Short 1975, Ridgely and Tudor 1989, 1994). Essentially monotypic species with little differentiation between populations include the White-breasted Tinamou (*Nothura boraquira*) and Chotoy Spinetail (*Schoeniophylax phryganophila*). Other species with more distinct racial differences include (races given in Chaco/Caatinga sequence): the Blue-crowned Parakeet (*Aratinga acuticaudata acuticaudata/hemmorhous*), Rufous Cachalote (*Pseudoseisura cristata unirufa/cristata*), Stripe-backed Antbird (*Myrmorchilus strigilatus suspicax/strigilatus*), White Monjita (*Xolmis irupero irupero/nivea*), Greater Wagtail-Tyrant (*Stigmatura budytoides inzonata/gracilis*) and Bay-winged Cowbird (*Molothrus badius badius/fringillarius*). Other examples occur at the species level. The concordance of this disjunct distribution pattern among species belonging to unrelated taxonomic groups implies a shared historical process of vicariance (e.g. Cracraft and Prum 1988). Although plausible, long-distance dispersal of a taxon across unfavorable Cerrado habitat from one side to the other is unlikely to occur in relatively sedentary taxa not known for long-distance migration (e.g. White-breasted Tinamou). Rather, a relatively recent vicariance event or series of events probably occurred, which subdivided a contiguous ancestral population into isolated Chaco and Caatinga units. Such an event likely occurred with *S. suiriri*. The most plausible agent for vicariance was the formation of humid forest barriers during previous interglacial periods (e.g. Haffer 1985, 1987; Willis 1992).

In conformity with the vicariance model of differentiation, I postulate the following scenario for differentiation in *S. suiriri*. Initially, an ancestral population of *S. suiriri* resembling nominate *suiriri* occupied the entire arid diagonal from the Chaco to the Caatinga. After one or more vicariance events isolated Chaco, Cerrado, and Caatinga populations, the Cerrado population differentiated more rapidly than the two peripheral isolates, eventually acquiring the traits of *affinis*. As the southern population of nominate *suiriri* spread northward and *affinis* spread southward, they met and

freely hybridized in the absence of isolating mechanisms, thus forming a hybrid swarm of individuals exhibiting intermediacy and increased variability. Because the population from the hybrid zone in northeastern Paraguay appears to be composed entirely of hybrids with few parental phenotypes (22 hybrid specimens vs. 2 purportedly typical *affinis*; Laubmann 1940, Zimmer 1955), little or no assortative mating occurred. Thus, the two forms appear to be conspecific when the criterion of reproductive isolation—a hallmark of the biological species concept (e.g. Mayr 1970)—is applied.

In the Caatinga, hybridization may also have occurred when *affinis* and the isolated remnant *suiriri* population came into contact, but the situation there remains less clear. Poorly known *bahiae* may have shared a most recent common ancestor with (1) an isolated population of *affinis* (Fig. 4A), (2) a remnant population of *suiriri* (Fig. 4B), or (3) may instead constitute a hybrid population of remnant *suiriri* × *affinis* (Fig. 4C). The proximity of *affinis* and the distant current distribution of *suiriri* support the first hypothesis; if that is true, the shared traits of *bahiae* and *suiriri* would have evolved independently. The second hypothesis is supported by the greater resemblance between *bahiae* and *suiriri* and the concordant pattern of disjunct Chaco–Caatinga taxa. The intermediate size and increased variability in plumage of the few *bahiae* specimens available, combined with descriptions of seemingly intermediate *affinis* × *bahiae* specimens in the region, support the third hypothesis of hybrid origin for *bahiae*. Indeed, the *bahiae* specimens exhibit a remarkable similarity with the *suiriri* × *affinis* hybrids from Paraguay; that was first noted by Zimmer (1955: 19), who stated that “some of the specimens of the intermediate population of northeastern Paraguay almost meet the requirements [of *bahiae*], but show, in most cases, too much of the yellowish basal area of the rectrices to agree fully.” If *bahiae* is indeed a hybrid taxon, as the morphological data suggest, it should not be considered a valid subspecies. Furthermore, it would appear to represent a disjunct hybrid population situated >1,000 km from the nearest current population of *suiriri*, a presumed parental phenotype, unless the white-bellied specimens tentatively assigned to *bahiae* actually represent a remnant *suiriri* population be-

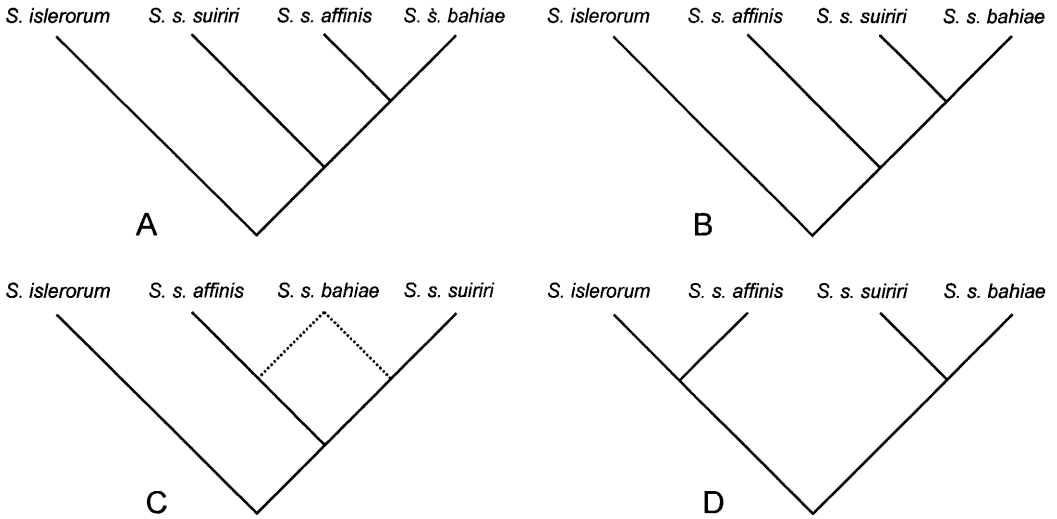


FIG. 4. Hypothetical relationships among *Suiriri* taxa illustrated by four cladograms. Note that *S. suiriri* is monophyletic in cladograms A–C and paraphyletic in cladogram D.

coming extinct through competition or introgression from *affinis* (e.g. Rhymer and Simberloff 1996). If indeed the white-bellied *bahiae* specimens represent a remnant *suiriri* population, then *bahiae* may be a distinct taxon less variable than it appears, represented exclusively by yellow-bellied birds. If that hypothesis is correct, *bahiae* may have shared a most recent common ancestor with either an isolated population of *affinis* or remnant *suiriri*. Finally, these hypotheses are based on the assumption of monophyly within *S. suiriri* (Fig. 4A–C). The superficial similarity between *S. islerorum* and *S. s. affinis* suggests that they may be sister taxa, in which case *S. suiriri* would be paraphyletic (Fig. 4D; McKittrick and Zink 1988 discuss the implications for species concepts), but *S. islerorum* appears behaviorally and vocally distinct (Zimmer et al. 2001). Genetic studies are clearly needed to elucidate further the relationships and history of differentiation among the forms of *S. suiriri* and *S. islerorum*.

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APPENDIX. Specimen number, sex, locality, date (1990s), and hybrid index score for three plumage color variables for all *Suiriri suiriri bahiae* and hybrid *S. s. suiriri* × *affinis* specimens examined in this study.

Specimen	Sex	Locality	Date (D-M-Y)	Plumage score		
				Back	Rump	Belly
<i>S. s. bahiae</i>						
AMNH 243914	♂	Belo Jardim, Pernambuco, Brazil	26-02-27	0	0	1
AMNH 243916	♂	Gilbúes/Pindaíba, Piauí, Brazil	11-06-27	0	0	0
AMNH 243917	♀	Gilbúes/Pindaíba, Piauí, Brazil	11-06-27	0	0	0
FMNH 64119	♀	Queimadas, Bahia, Brazil	12-08-13	0	0	2
<i>S. s. suiriri</i> × <i>affinis</i>						
AMNH 319815	?	Zanja Morotí, Concepción, Paraguay	03-09-30	1	0	2
AMNH 319812	♀	Zanja Morotí, Concepción, Paraguay	31-08-30	1	0	2
AMNH 319814	♀	Zanja Morotí, Concepción, Paraguay	03-09-30	1	0	1
AMNH 319811	♂	Zanja Morotí, Concepción, Paraguay	31-08-30	1	0	1
AMNH 319813	♂	Zanja Morotí, Concepción, Paraguay	03-09-30	1	0	1
AMNH 319808	♂	Zanja Morotí, Concepción, Paraguay	03-09-30	1	0	0
AMNH 319816	?	Zanja Morotí, Concepción, Paraguay	05-09-30	1	0	1
AMNH 321129	♀	San Luis de la Sierra, Concepción, Paraguay	12-05-31	1	0	2
AMNH 321128	♂	San Luis de la Sierra, Concepción, Paraguay	22-05-31	1	0	2
AMNH 321127	♂	San Luis de la Sierra, Concepción, Paraguay	16-05-31	1	0	2
AMNH 321123	♀	San Luis de la Sierra, Concepción, Paraguay	23-05-31	1	0	0
AMNH 321126	♂	San Luis de la Sierra, Concepción, Paraguay	15-05-31	1	0	2
AMNH 321125	♂	San Luis de la Sierra, Concepción, Paraguay	15-05-31	1	0	2
AMNH 321130	♀	San Luis de la Sierra, Concepción, Paraguay	15-05-31	1	0	2
AMNH 321124	♂	San Luis de la Sierra, Concepción, Paraguay	12-05-31	2	1	1
AMNH 321122	♂	San Luis de la Sierra, Concepción, Paraguay	18-05-31	1	0	0
AMNH 321131	♀	San Luis de la Sierra, Concepción, Paraguay	21-05-31	1	0	2
AMNH 319489	♂	Campanário, Mato Grosso do Sul, Brazil	07-07-30	1	2	2
CM 80363	♂	Río Quizer, Santa Cruz, Bolivia	07-06-18	1	1	0
CM 80364	♂	Río Quizer, Santa Cruz, Bolivia	07-06-18	1	1	0