

SYSTEMATICS OF THE TAWNY-BELLIED SEEDEATER (*SPOROPHILA HYPOXANTHA*). II. TAXONOMY AND EVOLUTIONARY IMPLICATIONS OF THE EXISTENCE OF A NEW TAWNY MORPH

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Abstract. The capuchinos, a subset of the genus *Sporophila*, represent a radiation of seedeaters characterized by little genetic differentiation, virtually no change in bill and body shape, marked plumage differences on a common theme, and notable differentiation in vocalizations and habitat use. We describe a distinctive variant that would have been considered a species by the traditional strictly phenotypical criteria for classification of species in the genus. This variant resembles the Tawny-bellied Seedeater (*S. hypoxantha*) but has a tawny, not gray, nape and back. It is also identical in pattern to the Chestnut Seedeater (*S. cinnamomea*) but has a tawny rather than chestnut body. We tested four hypotheses to assess the status of the variant: that it represents a new species, a hybrid *S. hypoxantha* × *S. cinnamomea*, a color morph of *S. cinnamomea*, or a color morph of *S. hypoxantha*. The variant is identical to *S. hypoxantha* in vocalizations and habitat use, varying geographically in parallel. Both forms breed syntopically, and the tawny variant is recorded only within the range of *S. hypoxantha*, with many records from areas where *S. hypoxantha* is the only breeding representative of the *ruficollis* group. We consider the tawny variant to be a color morph of *S. hypoxantha*. Two nontrivial evolutionary paths can constitute precursors to speciation in the capuchinos: (1) differentiation in vocalizations and habitat use arises with little plumage change in more or less geographically isolated populations, and (2) differentiation in plumage proceeds without change in vocalizations and habitat use within some populations.

Key words: *Sporophila*, *capuchinos*, *habitat*, *morph*, *radiation*, *regiolect*, *taxonomy*.

Sistemática de *Sporophila hypoxantha*. II. Taxonomía e Implicancias Evolutivas de la Existencia de una Nueva Forma en *Sporophila*

Resumen. Los capuchinos representan un conjunto de especies del género *Sporophila* proveniente de una radiación única de pequeños semilleros-fruteros. Esta radiación ha ocurrido con escasa diferenciación genética, virtualmente sin cambios en las formas del pico y cuerpo, marcadas diferencias en el plumaje sobre una base común y diferencias notables en sus vocalizaciones y uso de hábitat. Describimos una variante distintiva que hubiera sido considerada una especie con base en el criterio tradicional estrictamente fenotípico de asignación de especies en el género. Esta forma es similar a *S. hypoxantha*, pero con la nuca y la espalda naranjas en vez de gris. También tiene un patrón idéntico a *S. cinnamomea*, pero con cuerpo naranja en vez de castaño. Pusimos a prueba cuatro hipótesis sistemáticas para evaluar el status de esta variante: que representa una nueva especie, un híbrido *S. hypoxantha* × *S. cinnamomea*, un morfo de color de *S. cinnamomea* o un morfo de color de *S. hypoxantha*. La nueva variante es idéntica a *S. hypoxantha* en vocalizaciones y uso de hábitat, mostrando la misma variación geográfica en estas características. Ambas formas crían en sintopía y todos los registros de la nueva variante se presentaron dentro de los límites geográficos de *S. hypoxantha*, con varios registros en áreas donde *S. hypoxantha* es el único representante del grupo *ruficollis* que cría. Consideramos que la nueva variante es un morfo de color de *S. hypoxantha*. Dos trayectorias evolutivas no triviales pueden constituir precursores a la especiación en los capuchinos: (1) la diferenciación en vocalizaciones y uso de hábitat aparecen con escaso cambio en el plumaje en poblaciones más o menos aisladas geográficamente y (2) la marcada diferenciación en el plumaje aparece sin cambios en las vocalizaciones y en el uso de hábitat dentro de algunas poblaciones.

INTRODUCTION

The spectacular diversity of the neotropical seedeaters of the genus *Sporophila* poses several systematic and evolutionary dilemmas. The genetic differences among the 10 or 11 species constituting the subset known as the *capuchinos* seem to be very

shallow, impeding the phylogenetic reconstruction and evaluation of species limits in the group by that means (Lijtmaer et al. 2004, Kerr et al. 2009). Natural-history data, however, have proven useful in furnishing key evidence for the importance of vocalizations and habitat use in understanding the fast evolutionary radiation of the group (Areta 2008, 2010, Areta et al. 2011).

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A wealth of structurally uniform taxa constitute the capuchino group within *Sporophila*: the Dark-throated Seedeater (*S. ruficollis*), Rufous-rumped Seedeater (*S. hypochroma*), Chestnut Seedeater (*S. cinnamomea*), Marsh Seedeater (*S. palustris*), Tawny-bellied Seedeater (*S. hypoxantha*), Black-and-tawny Seedeater (*S. nigrorufa*), Capped Seedeater (*S. bouvreuil*, including *S. pileata* sensu Machado and Silveira [2011] and Areta [2010]), and the “gray-cheeked capuchinos,” the Ruddy-breasted Seedeater (*S. minuta*), Chestnut-bellied Seedeater (*S. castaneiventris*), and Black-bellied Seedeater (*S. melanogaster*) (Sick 1997, Lijtmaer et al. 2004, Areta et al. 2011). Moreover, three species are thought to be polymorphic in color: the Entre Ríos Seedeater (*S. “zelichi”*) is apparently a morph of *S. palustris* (Areta 2008), the black-collared “caraguata” form is presumably a morph of *S. ruficollis* (Areta et al. 2011), and the black “xumanxu” is a morph of *S. melanogaster* (Repenning et al. 2010b). There is little evidence that these variations represent hybrids and none that they represent valid species. These three morphs would have been considered species on the basis of traditional typological (plumage-based) criteria (e.g., Narosky 1977). Recent developments in the taxonomy of the capuchinos challenge this view and point to the value of vocalizations and patterns of habitat use as key features delimiting species on the basis of biological data (Areta 2008, 2010). This neotropical box of Pandora has barely started to show its surprises.

Among the capuchinos, *S. hypoxantha* is characterized by tawny throat, belly, rump, and auriculars and gray cap, nape, and back, with wide variation in color saturation (Figs. 1, 2). It is one of the most widespread members of the group, ranging from central-eastern and northwestern Argentina to eastern Uruguay, southeastern and southwestern Brazil, Paraguay, and eastern Bolivia (Short 1969, 1975, Ridgely and Tudor 1989). This fairly large distribution is not continuous, the species being present only in suitable grasslands, and this patchiness has presumably led to the development of diagnostic vocal regiolects (Areta and Repenning 2011). No consistent geographic variation has been described in the species’ plumage, and no subspecies within *S. hypoxantha* have been described. However, our field work in the grasslands of Argentina and Brazil demonstrates the unexpected existence of a hitherto undescribed distinct plumage form that occurs at widely separated localities. This new form has tawny body and a gray cap, thus resembling the chestnut-bodied and gray-capped *S. cinnamomea* and the tawny-bellied and gray-backed *S. hypoxantha* (Figs. 1, 2).

In this work we (1) describe in detail the new tawny form of capuchino for which we coin the informal name “uruguay,” (2) assess its systematics by testing four hypotheses based on habitat use and vocalizations, and (3) discuss its evolutionary implications.

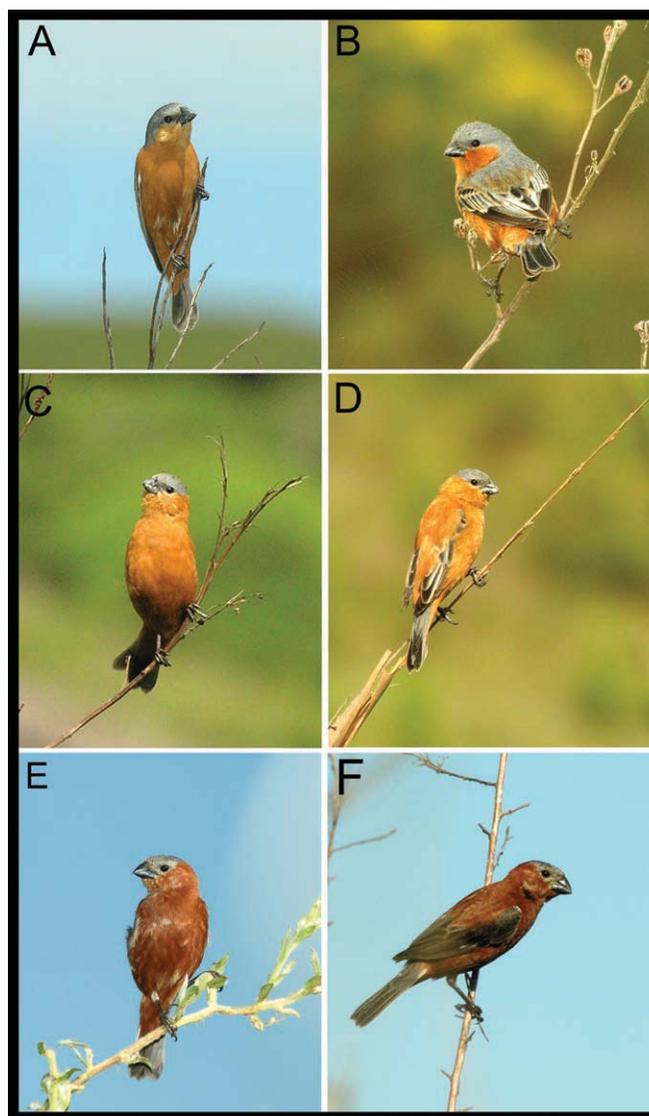


FIGURE 1. Adult males of the forms studied in this work. Typical adult male of the Tawny-bellied Seedeater (*Sporophila hypoxantha*), ventral (A) and dorsal (B); Coxilha Rica, Lages, Santa Catarina, Brazil. Adult male of the “uruguay” form, ventral (C) and dorsal (D); Antiga Estação Ferroviária, Bom Jesus, Rio Grande do Sul, Brazil. Adult male of the Chestnut Seedeater (*S. cinnamomea*), ventral (E) and dorsal (F); Distrito de Areal, Quaraí, southwestern Rio Grande do Sul, Brazil. Photos by M. Repenning.

METHODS

GEOGRAPHIC AND TIME COVERAGE

We searched for capuchinos during seven breeding seasons from October 2003 to April 2009. Sampling effort totaled 227 days in the field, with 33 days at 11 locations in Entre Ríos (Argentina), 28 days at 7 locations in Corrientes (Argentina), 3 days at 2 locations in Santa Fé (Argentina), 2 days at 1 location in Formosa (Argentina), 3 days at 2 locations in Paysandú

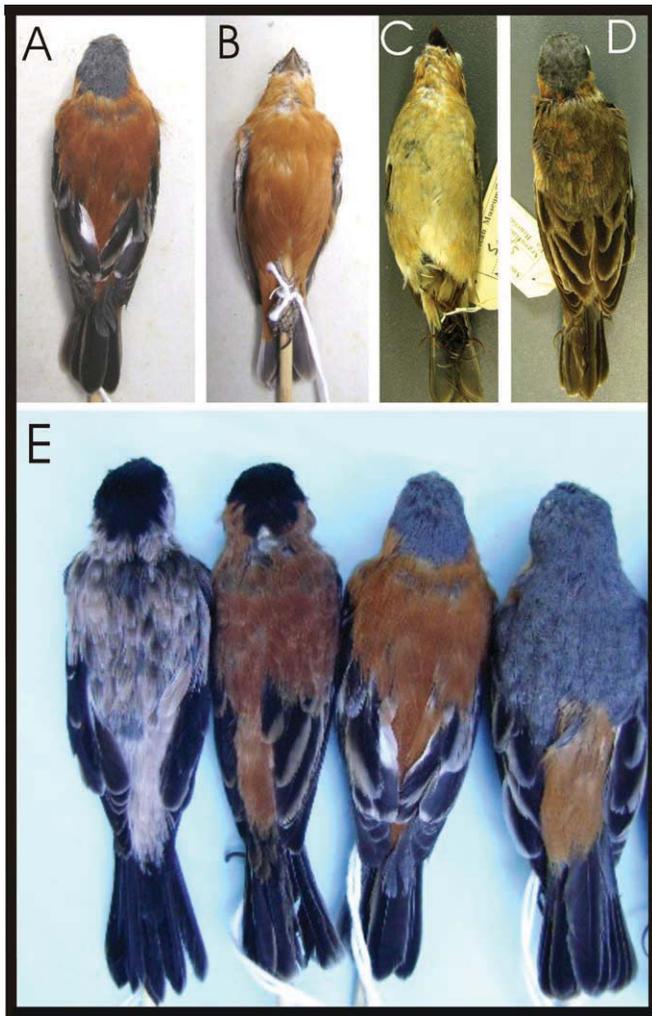


FIGURE 2. Museum specimens of the “uruguaya” form and comparison with the Southern Capped Seedeater (*S. [bouvreuil] pileata*), Northern Capped Seedeater (*S. [bouvreuil] bouvreuil*), and Tawny-bellied Seedeater (*S. hypoxantha*). (A) ventral and (B) lateral view of adult male “uruguaya,” AMNH 798521, Arapotí, Paraná, Brazil; (C) ventral and (D) lateral view of subadult male “uruguaya,” MHNCI 5207, Estancia Rincón de Luna, Corrientes, Argentina; (E) from left to right, dorsal views of adult male specimens of *S. b. pileata*, *S. b. bouvreuil*, “uruguaya,” and *S. hypoxantha* (MHNCI specimens).

(Uruguay), 3 days at 3 locations in Rocha (Uruguay), 3 days at 2 locations in Santa Cruz (Bolivia), 3 days at 1 location in Beni (Bolivia), 85 days at 10 locations in Rio Grande do Sul (Brazil), 70 days at 5 locations in Santa Catarina (Brazil), and 4 days at 1 location in Paraná (Brazil) (Fig. 3).

MORPHOLOGY

We base our description and analysis of the plumage of “uruguaya” on field observations of live birds, evaluation of photographs, and examination of one adult and one subadult museum specimen. The description of the color of the adult

specimen follows the Naturalist’s Color Guide (Smithe 1975) (Fig. 2). We studied the plumages and measured the bill length (exposed culmen), wing chord, tail length, and tarsus length of 56 specimens of *S. hypoxantha*, two of “uruguaya” and 9 of *S. cinnamomea* (Appendix 1). Given the small sample of specimens of “uruguaya” and the uniformity in measurements within the capuchinos (Areta et al. 2011), we avoided any statistical comparison.

HABITAT USE

To characterize habitat use on a regional scale, we assigned each territorial bird to one of 13 broad habitat categories (see Areta and Repenning 2011 for detailed descriptions). These habitat types are widely distributed and may coexist as a mosaic at a single locality or within a limited geographic (i.e., several habitats may interdigitate at the same locality). Although the broad habitat categories used may mask subtle differences that could indicate habitat segregation between sympatric forms at a finer scale, they were designed to apply over a wide area where more detailed descriptions of habitats would have precluded the discovery of any habitat-use pattern because many features unique to each site would have masked overall similarities among sites (see sampling localities in Appendix 2). We consider each contact to be an independent sample appropriate for evaluation of habitat preference. We defined preferred habitat as the habitat where we found at least 65% of the territorial males of each regiolect. We evaluated habitat preference by comparing the frequency of occurrence of each population in each habitat.

BIRD VOCALIZATIONS

We recorded vocalizations with various microphones (Sennheiser ME-62 mounted on a Telinga Universal Parabola or on a 60-cm parabola) and tape recorders (Marantz PMD-222, PMD-661, and Sony TC-D5M). We prepared spectrograms with Syrinx 2.1 (J. Burt, www.syrinxpc.com). All our recordings are archived at the Macaulay Library of Natural Sounds (Cornell Lab of Ornithology, Ithaca, New York). See Appendix 3 for data.

To examine differences and similarities in vocalizations among populations, we first characterized notes which, on the basis of shape (including duration and frequency distribution) and relative position in the songs, could be identified unambiguously despite variation among individuals. We then compared the frequency of occurrence of these notes in individuals within and among populations. Our analysis was limited to sexually mature males.

SYSTEMATIC HYPOTHESES

In accordance with previous works (Areta 2008, Areta et al. 2011), we tested four hypotheses to evaluate the taxonomic status of the “uruguaya” form. To avoid unconscious preference for any systematic hypothesis, we used the method of multiple working

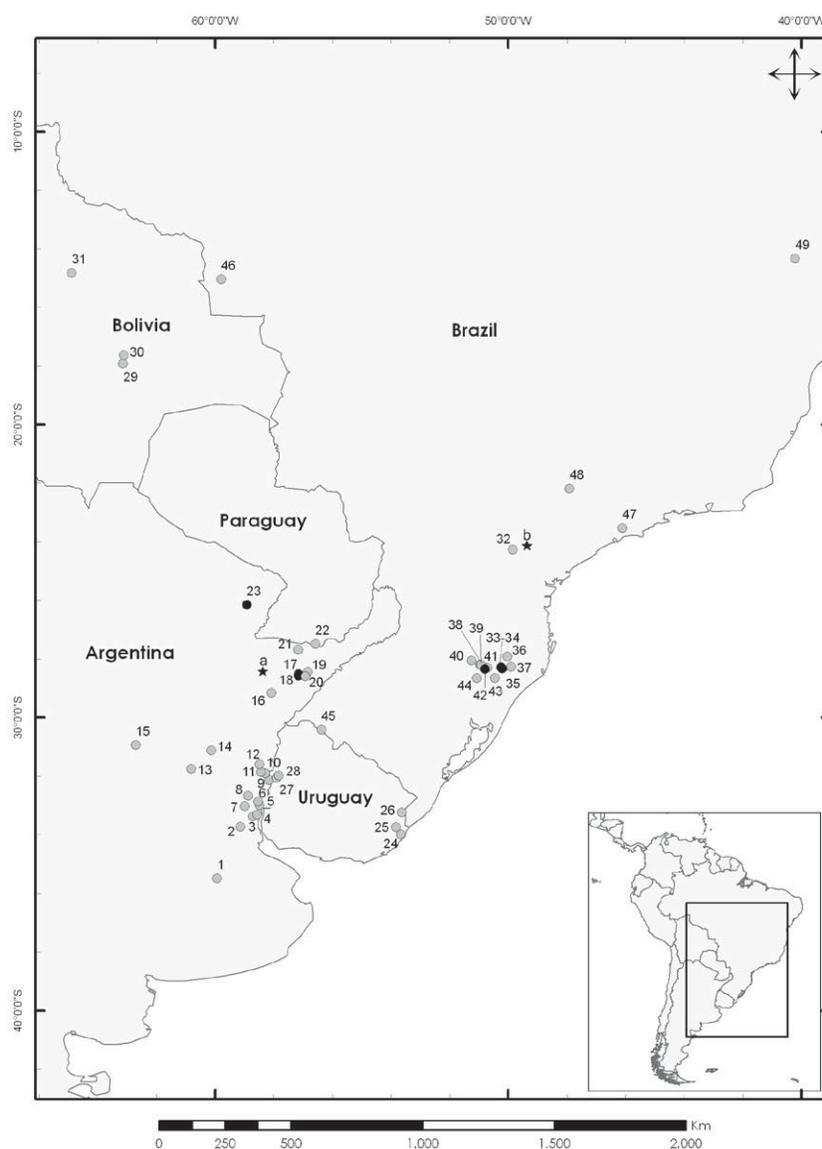


FIGURE 3. Geographic location of important sites for this study. Numbers and circles indicate localities visited during this study (black circles where “uruguayana” has been recorded), letters and stars indicate localities not visited during this study where specimens of “uruguayana” have been collected. **Argentina, Buenos Aires:** 1, Saladillo (59° 56' W, 35° 30' S). **Entre Ríos:** 2, Ibicuy (59° 09' W, 33° 44' S); 3, Arroyo Nancay (58° 44' W, 33° 23' S); 4, Estancia La Marita (58° 35' W, 33° 20' S); 5, Gualeguaychú (58° 30' W, 33° 00' S); 6, Las Piedras (58° 33' W, 32° 53' S); 7, Larroque (59° 00' W, 33° 02' S); 8, Urdinarrain (58° 53' W, 32° 41' S); 9, Pto. Liebig and Arroyo Caraballo (58° 11' W, 32° 09' S); 10, Parque Nacional El Palmar (58° 18' W, 31° 55' S); 11, Arroyo Baru (58° 27' W, 31° 52' S); 12, San Salvador (58° 30' W, 31° 37' S). **Santa Fé:** 13, Sauce Viejo (60° 50' W, 31° 46' S); 14, Campo del Medio (60° 08' W, 31° 08' S). **Córdoba:** 15, Laguna Mar Chiquita (62° 43' W, 30° 57' S). **Corrientes:** a, Estancia Rincón de Luna (28° 28' S, 58° 14' W); 16, Mercedes (58° 05' W, 29° 10' S); 17, Estancia Rincón del Socorro (57° 10' W, 28° 32' S); 18, Colonia Pellegrini (57° 10' W, 28° 35' S); 19, Cambá Trapo (56° 51' W, 28° 27' S); 20, Cuenca del Río Aguapey (56° 56' W, 28° 36' S); 21, Estancia San Juan Poriahú (57° 11' W, 27° 42' S)/Parque Nacional Mburucuyá (58° 05' W, 28° 00' S); 22, Rincón Santa María (56° 35' W, 27° 30' S). **Formosa:** 23, Estancia El Bagual (58° 56' W, 26° 10' S). **Uruguay, Rocha:** 24, Laguna Negra (53° 40' W, 34° 00' S); 25, Bañados de la India Muerta (53° 50' W, 33° 45' S); 26, Cebollatí (53° 38' W, 33° 15' S). **Paysandú:** 27, Lorenzo Geyres, Quebracho (57° 55' W, 32° 04' S); 28, Queguayar (57° 50' W, 32° 00' S). **Bolivia, Santa Cruz:** 29, Lomas de Arena (63° 10' W, 17° 56' S); 30, Pampas de Viru-Viru (63° 08' W, 17° 39' S). **Beni:** 31, Trinidad-Mamoré (64° 54' W, 14° 50' S). **Brazil, Paraná:** b, Arapotí, Jaguaiaíva (24° 09' S, 49° 49' W); 32, Fazenda Chapadão–Rio das Perdizes (49° 51' W, 24° 17' S). **Santa Catarina:** 33, Coxilha Rica/Estancia do Meio (50° 15' W, 28° 18' S); 34, Estancia do Meio (50° 15' W, 28° 18' S); 35, Rio São Mateus (50° 13' W, 28° 21' S); 36, Pedra Branca (50° 02' W, 27° 55' S); 37, São Joaquim/Lages (49° 55' W, 28° 17' S). **Rio Grande do Sul:** 38, Capão Alto (50° 58' W, 28° 12' S); 39, São Pedro (50° 56' W, 28° 13' S); 40, Capão Bonito (51° 16' W, 28° 04' S); 41, Antiga Estação Férrea–Bom Jesus (50° 44' W, 28° 19' S); 42, Fazenda Socorro/Rio Santana (50° 48' W, 28° 22' S); 43, Cachoeira dos Baggio (50° 28' W, 28° 40' S); 44, Guacho (51° 05' W, 28° 40' S); 45, Distr. Areal-Quaraí (56° 23' W, 30° 26' S). **Mato Grosso:** 46, Campos do Encanto–Vila Bela da Santíssima Trindade (59° 48' W, 15° 03' S). **São Paulo:** 47, Mogi das Cruzes (46° 07' W, 23° 33' S); 48, Estação Ecológica Itirapina (47° 55' W, 22° 12' S). **Bahia:** 49, Boa Nova (40° 13' W, 14° 21' S).

hypotheses (Chamberlin 1965). We deduced predictions for each hypothesis on the basis of the recognition species concept (Paterson 1985), in which any bird species must have a preferred or normal habitat and a specific mate-recognition system that ensures successful reproductive encounters between the sexes (Paterson 1985, Vrba 1995). Habitat-dependent selection acting on the specific mate-recognition system is thus the main force thought to influence speciation, and two closely related valid species should not share the same preferred habitat. We considered vocalizations to be a key element in species-specific recognition (i.e., a crucial part of the specific mate-recognition system). See Slabbekoorn and Smith (2002) for a review of habitat-dependent divergence in vocalizations and speciation. We used the recognition species concept to evaluate the specific status of the capuchinos (Paterson 1985, Eldredge 1995, Haffer 1997) because this concept clearly delimits species and narrows the meaning of the word species to a restricted biological phenomenon, permits the testing of predictions, and makes the results of our study easily interpretable by researchers endorsing other species concepts. Although many species of *Sporophila* coexist in the same habitats, they do not regularly appear to be each others' closest relatives. The species of capuchinos that we studied are one another's closest relatives and do not differ obviously in beak morphology. The differences among these capuchinos are found in the males' plumage, songs, and preferred habitat (Areta 2008, Areta et al. 2011). Therefore, although voices alone might serve to assess the specific status of populations, a strong test of specific identity should test voice and distinctive habitat as key features of any valid species of capuchino.

The hypotheses that we tested were (Fig. 1, Table 1):

(1) Good-species hypothesis: "uruguaya" is a valid species on the basis of its diagnostic plumage pattern. If so, we predicted that birds of this plumage should have vocalizations and a preferred habitat differing from those of other closely related species.

TABLE 1. Four alternative hypotheses and predictions that allow for an evaluation of the systematic status of the "uruguaya" form. For each prediction, support is indicated by (+), rejection by (–) and inconclusive evidence by (±).

Hypothesis	Predictions regarding "uruguaya"	
	Vocalizations	Preferred habitat
1. Good species	Unique (–)	Unique (–)
2. Hybridization	Intermediate between <i>S. hypoxantha</i> and <i>S. cinnamomea</i> (–) or identical to <i>S. hypoxantha</i> (+) or <i>S. cinnamomea</i> (–)	Shared by both <i>S. hypoxantha</i> and <i>S. cinnamomea</i> (–)
3. Color morph I	Same as <i>S. cinnamomea</i> (–)	Same as <i>S. cinnamomea</i> (–)
4. Color morph II	Same as <i>S. hypoxantha</i> (+)	Same as <i>S. hypoxantha</i> (+)

(2) Hybridization hypothesis: "uruguaya" is a hybrid between *S. hypoxantha* and *S. cinnamomea*, based on the possibility that the tawny back and collar of "uruguaya" might originate through hybridization of the chestnut-bodied *S. cinnamomea* with the gray-backed and tawny-bellied *S. hypoxantha*. If so, we predicted that the songs of "uruguaya" should either be intermediate between those of *S. hypoxantha* and *S. cinnamomea* (if songs are genetically determined) or identical to that of the paternal species (*S. hypoxantha* or *S. cinnamomea*, if songs are learned from the father). This hypothesis predicts that the habitat of "uruguaya" should be shared by both parental forms (*S. hypoxantha* and *S. cinnamomea*).

(3) Color-morph hypothesis I: "uruguaya" is a color morph of *S. cinnamomea*, since the two forms have the back and nape of the same color of the belly (chestnut in *S. cinnamomea* and tawny in "uruguaya"). If so, we predicted that "uruguaya" should have songs and preferred habitats like those of *S. cinnamomea*.

(4) Color-morph hypothesis II: "uruguaya" is a color morph of *S. hypoxantha*, since both have tawny underparts. If so, "uruguaya" should have songs and preferred habitats like those of *S. hypoxantha*.

RESULTS

DESCRIPTION OF THE "URUGUAYA" FORM

Adult males. The following description is based on Museu de História Natural Capão da Imbuia (MHNCI) 5207, collected 15 September 1999 at Arapotí, Paraná, Brazil, by Eduardo Carrano (Figs. 2A, B). Forehead and crown Medium Neutral Gray (Bluish) forming a hood down to mid-eye level, with a few small white feathers below the eye. Auriculars, nape, chin, throat, sides of neck, and breast Orange Rufous and Tawny. Back, flanks, abdomen, rump, and under-tail coverts Tawny and Cinnamon-Rufous. Edges of upper-tail coverts Medium Neutral Gray. Primaries and secondaries blackish, paler on the outer vane. From the base to the middle of the primaries and secondaries a white spot forms a speculum, especially on the upper wing. Tertiaries Blackish Neutral Gray with outer vane edged Light Neutral Gray or Mikado Brown. Wing coverts Blackish edged Medium Neutral Gray. Rectrices dorsally Blackish, somewhat paler on the underside. Original tarsus and bill colors not confirmed (label data seem inaccurate, stating tarsus "ochre" and bill "ochre"). In dried specimen bill color Sepia with base of lower mandible Pale Pinkish Buff.

Three males, one photographed on 12 November 2006 at Antiga Estação Ferroviária, Bom Jesus Municipality, Rio Grande do Sul, Brazil (Fig. 1), one tape-recorded and observed on 28 February 2009 and another photographed and collected on 12 January 2010 in the valley of the Lava-Tudo River/Coxilha Rica, Santa Catarina, Brazil, were the same in color. They had a light bluish-gray forehead and crown forming a hood down to mid-eye level, with a few small white feathers below the eye. Auriculars, nape, chin, throat, sides of neck, back, breast,

flanks, abdomen, rump, and under-tail coverts uniform light brownish orange. Edges of upper-tail coverts gray. Primaries and secondaries blackish on the outer vane, and paler on the inner vane. Large white speculum in the central portion of primaries and secondaries. Tertiaries blackish with outer vane edged withish gray. Wing coverts blackish edged gray. Rectrices blackish. Tarsus brownish black. Bill blackish.

We photographed a typical male adult of “uruguayaya” on 8 January 2005 at the Estancia Rincón del Socorro, Corrientes, Argentina. I. Roesler observed another adult male on 15 October 2009 at the same locality, and we tape-recorded and photographed it on 18 October 2009. Roesler photographed another adult male on 15 October 2009 between Mercedes and Colonia Pellegrini, Corrientes, Argentina.

An adult male of “uruguayaya” photographed at El Bagual, Formosa, Argentina, by Alejandro Di Giacomo resembled those described above, differing only by its darker overall coloration, demonstrating color variation in “uruguayaya” paralleled by that within *S. hypoxantha*. Presumably this was the same individual we observed on 11 December 2006 at the same locality.

Young male/eclipse plumage. The following description is based on American Museum of Natural History (AMNH) 798521, collected 29 October 1961 at Estancia Rincón de Luna, Corrientes, by William Partridge (Figs. 2C, D). Forehead and crown light bluish gray, forming a hood down to mid-eye level, with a few small white feathers below the eye. Auriculars, nape, chin, throat, and sides of neck uniform light orange, forming a complete collar. Breast, flanks, abdomen, and under-tail coverts light creamy-buff. Back and rump light brownish with some light orange feathers intermingled in the back. Upper-tail coverts brown. Primaries and secondaries blackish-brown. Large white speculum in the central portion of primaries and secondaries. Tertiaries blackish brown with outer vane edged whitish buff. Wing coverts blackish brown edged whitish buff. Rectrices blackish brown. Tarsus brownish black. Bill blackish.

The overall pattern that will be present in the adult is discernible even in the young bird, a situation common to all the collared capuchinos (Areta 2010): the cap is mature, and the collar is ahead of the rest of the body in maturation exactly as

in the rest of the capuchinos. While the warm-orange collar extends onto the nape, the back shows some orange feathers mixed with the typical brown of juveniles and females. This pattern is also found in older males molting in or out of eclipse plumage (Areta et al. 2011).

Females. A female paired with a male “uruguayaya” at Estancia Rincón del Socorro was photographed on 18 October 2009, and another was accompanying the male along the Lava-Tudo River on 12 January 2010. We are unable to find any diagnostic feature distinguishing it from other females of the *ruficollis* group.

MORPHOLOGY

Measurements of the bill length, wing chord, tail length, and tarsus length of the two specimens of “uruguayaya” do not differ consistently from those of *S. hypoxantha* or *S. cinnamomea* and are within the ranges of variation of these species (Table 2, Appendix 1).

DISTRIBUTION AND ABUNDANCE

The “uruguayaya” form is known from seven localities, four in Argentina and three in Brazil: El Bagual, Formosa, Argentina (26° 10' S, 58° 56' W), Estancia Rincón de Luna, Corrientes, Argentina (28° 28' S, 58° 14' W), Estancia Rincón del Socorro, Corrientes, Argentina (28° 32' S, 57° 10' W), between Colonia Pellegrini and Mercedes, Corrientes, Argentina (28° 35' S, ~ 57° 10' W), Antiga Estação Ferrea near the mouth of Rio Santana, Bom Jesus, Rio Grande do Sul, Brazil (28° 19' S, 50° 44' W), Coxilha Rica, ~90 km south of Lages, Santa Catarina, Brazil (28° 18' S, 50° 16' W), and Arapotí, Jaguariaíva, region of the Campos Gerais, Paraná, Brazil (24° 09' S, 49° 49' W). It is also known from neighboring areas in Uruguay (J. C. Mazulla, in litt.). We suspect that the migratory movements of “uruguayaya” are indistinguishable from those of syntopic populations of *S. hypoxantha* (see Areta and Repenning 2011).

The “uruguayaya” form is exceedingly rare: we found only six individuals in the field, while similar search efforts returned over 400 territorial males of *S. hypoxantha*. During a single breeding season in the Campos de Cima da Serra,

TABLE 2. Measurements of the Tawny-bellied Seedeater (*Sporophila hypoxantha*), “uruguayaya” form, and Chestnut Seedeater (*S. cinnamomea*). Values (mm) are mean \pm SD [range] (*n*). Data from Appendix 1.

	Exposed culmen	Wing chord	Tail length	Tarsus length
<i>S. hypoxantha</i>	8.0 \pm 0.5 [6.9–8.9] (56)	52.9 \pm 1.7 [51.0–56.5] (56)	38.4 \pm 1.9 [34.9–42.0] (54)	14.0 \pm 0.6 [12.5–15.0] (54)
“Uruguayaya” form	8.0 \pm 0.2 [7.9–8.2] (2)	52.3 \pm 1.3 [51.0–53.5] (2)	37.2 \pm 2.8 [35.0–39.0] (2)	13.9 \pm 0.6 [13.2–14.5] (2)
<i>S. cinnamomea</i>	8.4 \pm 0.4 [7.5–9.1] (9)	52.8 \pm 1.7 [51.0–54.5] (9)	37.25 \pm 0.87 [36.0–38.0] (4)	13.7 \pm 0.7 [12.6–14.4] (9)

we found a single territorial “uruguaya” and 95 territories of typical *S. hypoxantha* and saw another male in a flock with >100 *Sporophila* seedeaters, of which ~40 were males of *S. hypoxantha*.

HABITAT USE

We found “uruguaya” in *campos altos* in Formosa, Argentina (*n* = 1), in shrubby grasslands in Corrientes, Argentina (*n* = 2), in valley shrubby grasslands of the Campos de Cima da Serra in Rio Grande do Sul and Santa Catarina, Brazil, and in the Campos Gerais, Paraná, Brazil (*n* = 3) (Table 3). These are habitats of *S. hypoxantha* (Areta and Repenning 2011). No habitat data are available for any museum specimen of “uruguaya,” although both specimens were collected in localities where *S. hypoxantha* is known to breed.

At El Bagual (Formosa), a male “uruguaya” was feeding gregariously with *S. hypoxantha* in dry grassland of *Elionurus muticus*, *Imperata brasiliensis*, and *Andropogon lateralis* (*campos altos*). The area was crowded with at least eight territories of *S. hypoxantha*, but we were unable to locate the territory of the male “uruguaya.” A territorial male at Estancia Rincón del Socorro (Corrientes) responded aggressively to playback of males of *S. hypoxantha* of the Corrientes regiolect (see Vocalizations), as also did the female that held the territory with him. Both chased away two males of *S. hypoxantha* that had adjoining territories in the same dry shrubby grassland. A nonterritorial male at the same locality, was in a mixed-species flock with two of *S. hypoxantha*, one adult *S. cinnamomea*, two of *S. hypochroma*, three adults of *S. palustris*, and at least 14 juvenile/female birds. It was an extremely hot day, and the group had taken shelter from the sun in a stand of small native trees and bushes amid the grasslands. Another territorial male near Rio Santana (Rio Grande do Sul) sang intensively and defended its territory, responding aggressively to playback of voices of *S. hypoxantha* of the southern Brazil regiolect (see Vocalizations). The territory was on relatively dry soil in mountainous

terrain with several shrubs (e.g., *Baccharis* spp., *Vernonia chamaedris*, and *Eupatorium* spp.) of low to medium height (1–1.4 m) in a matrix of grassland dominated by *Saccharum angustifolium*. This territory was located amid three territories of typical *S. hypoxantha*. Both males observed at Coxilha Rica (Santa Catarina) occupied identical habitat, especially in regard to the structure of vegetation. Thus we clearly found “uruguaya” in full breeding syntopy with *S. hypoxantha* across its distribution.

VOCALIZATIONS

We recorded a single male of “uruguaya” at Estancia Rincón del Socorro, Corrientes, Argentina (Fig. 4), whose song was identical to males of *S. hypoxantha* of the Corrientes regiolect (Table 4). The introduction and 6 of the 13 notes identified in this regiolect of *S. hypoxantha* were also present in the recordings of this individual (Fig. 4; see Areta and Repenning 2011 for details). This male responded strongly to playback of the local regiolect of *S. hypoxantha* but ignored playback of voices of *S. cinnamomea* and *S. hypochroma*.

We recorded two individuals of “uruguaya” at Coxilha Rica, Santa Catarina, Brazil (Fig. 5), whose songs were indistinguishable from those of birds of the southeast Brazil regiolect of *S. hypoxantha* (Table 4). The introduction and 19 of the 22 notes identified in this regiolect of *S. hypoxantha* were also present in the songs of the two examples of “uruguaya” (Fig. 5, see Areta and Repenning 2011 for details). These two males responded immediately and aggressively to playback of voices of the local regiolect of *S. hypoxantha*.

HYPOTHESIS TESTING

We tested the four systematic hypotheses on the basis of these data, on those by Areta and Repenning (2011) for *S. hypoxantha*, and on those by Areta (2008) and Areta et al. (2011) for *S. cinnamomea*, synthesized in Tables 3 and 4.

The hypothesis that “uruguaya” is a valid species is rejected by both song and habitat data, since there are no

TABLE 3. Comparison of habitat use of adult males by regiolect of the “uruguaya” form, Tawny-bellied Seedeater (*S. hypoxantha*), and Chestnut Seedeater (*S. cinnamomea*).

Form: regiolect (<i>n</i>)	Habitat							
	<i>Caraguatal-cardal</i>	Undulating grassland	<i>Campos altos</i>	Shrubby grassland	Highland dry grassland	<i>Campos bajos</i>	Lowland wet	Highland wet
<i>S. hypoxantha</i> : Formosa(25)			72%			28%		
“Uruguaya”: Formosa (1)			100%					
<i>S. hypoxantha</i> : Corrientes (36)				89%			11%	
“Uruguaya”: Corrientes (2)				100%				
<i>S. hypoxantha</i> : SE Brazil (95)					41%			59%
“Uruguaya”: SE Brazil(3)					100%			
<i>S. cinnamomea</i> (34)	11.7%	73.5%					14.7%	

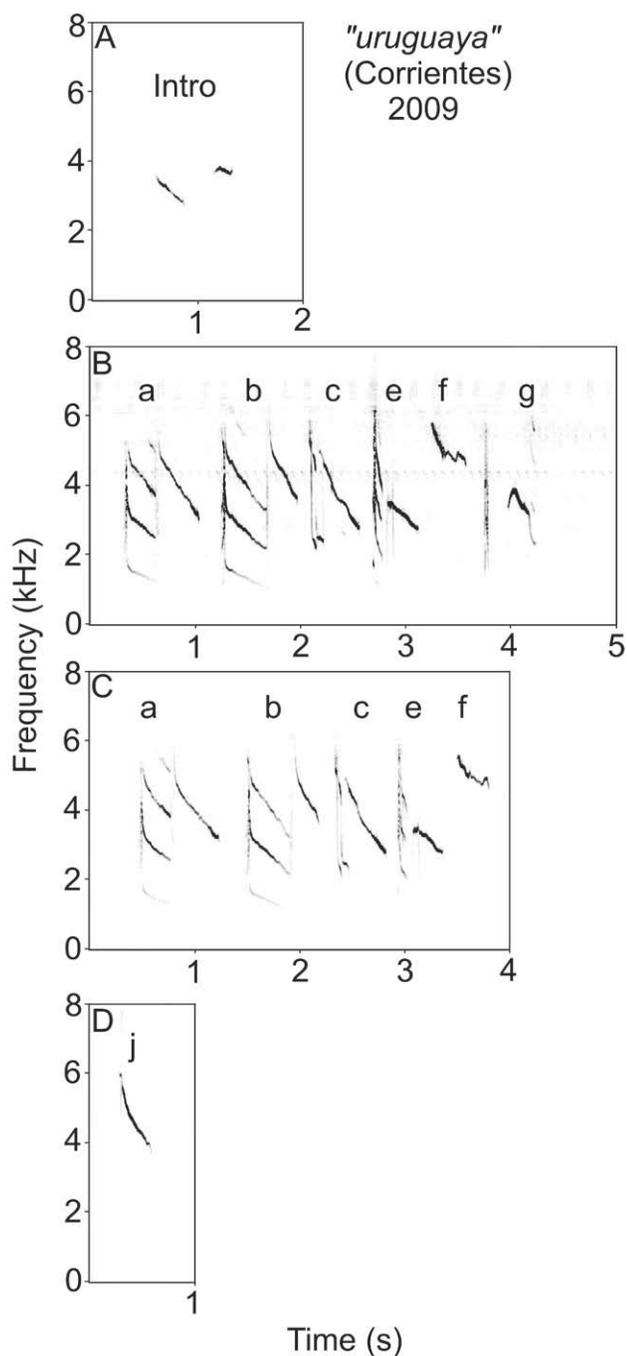


FIGURE 4. Spectrograms of vocalizations of the “uruguaya” form recorded 18 October 2009 at Estancia Rincón del Socorro, Corrientes, Argentina. These vocalizations are indistinguishable from those of the Tawny-bellied Seedeater (*S. hypoxantha*) from the same area (see Areta and Repenning 2011). (A) Introductory notes, (B, C) song, and (D) another note.

species-specific notes in its songs and no species-specific habitat (Table 1). There are no notes in the song of “uruguaya” (Figs. 4, 5, Table 4) that distinguish it from *S. hypoxantha*, and the two forms occupy the same habitat at the same localities (Table 3). On the other hand,

S. cinnamomea differs from “uruguaya” in both voice (Fig. 6) and preferred habitat (undulating grasslands, Table 3), exemplifying expected species-specific differences in habitat and vocalizations.

The hypothesis that “uruguaya” is a hybrid *S. hypoxantha* × *S. cinnamomea* is rejected by both song and habitat data (Table 1). Because there is no sign of intermediacy in the vocalizations of “uruguaya” between its putative parental forms *S. hypoxantha* and *S. cinnamomea*, the mixed-voice prediction is rejected (Figs. 4 and 5 vs. Fig. 6, Table 4). However, if songs were inherited or learned exclusively from fathers, similarities between songs of *S. hypoxantha* and “uruguaya” would be expected even if the latter is a hybrid. If “uruguaya” is of hybrid origin and songs are learned from the father, then evidence suggests that *S. hypoxantha* is always the paternal form. According to our data, habitat overlap between the proposed parental forms *S. cinnamomea* and *S. hypoxantha* is nil (Table 3), and presumably it is insufficient to allow hybridization where the two species’ distributions overlap; we found no “uruguaya” in the typical undulating grassland habitat of *S. cinnamomea* in the mesopotamian grasslands (Entre Ríos and Corrientes). Moreover, the populations of *S. hypoxantha* in the Humid Chaco (Formosa), Campos de Cima da Serra (Rio Grande do Sul and Santa Catarina), and Campos Gerais (Paraná) that we studied are allopatric from breeding populations of *S. cinnamomea*, hence no interbreeding should be possible. Thus voice, habitat use, and distribution suggest that *S. cinnamomea* is not important in the origin of “uruguaya.” None of the predictions of this hypothesis was supported by our results.

The hypothesis that “uruguaya” is a color morph of *S. cinnamomea* is rejected on the basis of both song and habitat data (Table 1). The songs of “uruguaya” and *S. cinnamomea* differ in note structure, pace, and duration (Figs. 4 and 5 vs. Fig. 6, Table 4). In addition, there is little habitat overlap between “uruguaya” and *S. cinnamomea*, and we found no “uruguaya” in the preferred habitat of *S. cinnamomea* (Table 3). Moreover, only three (all in Corrientes) of the seven known localities of “uruguaya” lies within the breeding range of *S. cinnamomea*, evidence against its being a morph of that species.

The hypothesis that “uruguaya” is a color morph of *S. hypoxantha* is supported by both song and habitat data (Table 1). The repertoire of “uruguaya” was a subset of that of corresponding regiolects of *S. hypoxantha* that were more intensively sampled (Figs. 4, 5, Table 4, see also Areta and Repenning 2011). Both “uruguaya” and *S. hypoxantha* were in the same habitats and in syntopy everywhere we found “uruguaya” (Table 3).

DISCUSSION

SYSTEMATICS OF THE “URUGUAYA” FORM

The new “uruguaya” form occurs with *S. hypoxantha*, and the similarities in habitat use, voices, and plumage features support its being a morph of *S. hypoxantha* and not a good distinct species, a hybrid of *S. hypoxantha* and *S. cinnamomea*, or a

TABLE 4. Comparison of note types and percentage of individual adult males in regiolects of the “uruguaya” form, Tawny-bellied Seedeater (*S. hypoxantha*) and Chestnut Seedeater (*S. cinnamomea*), whose songs included those notes. Letters correspond to spectrograms in Figures 4 and 5 for “uruguaya” (see Areta and Repenning [2011] for spectrograms of *S. hypoxantha* and Figure 6 for *S. cinnamomea*), and indicate homologous notes within regiolects and through time, but do not imply homologous notes between regiolects or forms.

Note type	Corrientes regiolect (<i>n</i>)		SE Brazil regiolect (<i>n</i>)		<i>S. cinnamomea</i> (<i>n</i>)	
	<i>S. hypoxantha</i> (24)	“Uruguaya” (1)	<i>S. hypoxantha</i> (33)	“Uruguaya” (2)	1991–1993 (4)	2003–2007 (20)
Introduction	79.2	100	93.9	100		
a	79.2	100	78.8	100	100	65
b	70.8	100	72.7	100	100	65
c	70.8	100	66.7	100	100	55
d	70.8		90.9	100	75	65
e	79.2	100	90.9	100	75	65
f	54.2	100	75.8	100	100	65
g	58.3	100	33.3		75	65
h	33.3		81.8	100	75	65
i	62.5		84.8	100		55
j	66.7	100	84.8	100	75	65
k	41.7		78.8	100		50
l	12.5		66.7	100		
m	29.3		39.4	100		
n			57.6	100		
o			66.7	100		
p			24.2			
q			21.2	100		
r			57.6	100		
s			9.1	100		
t			36.4	100		
u			24.2	100		
v			6.1			

morph of *S. cinnamomea*. The occurrence of “uruguaya” in areas where *S. hypoxantha* is the only breeding capuchino is further evidence of its being a morph of *S. hypoxantha*, and its presence in areas where *S. cinnamomea* is not known to breed refutes the hypotheses that it arose through hybridization or that it is a morph of *S. cinnamomea*. The low abundance at which “uruguaya” occurs in nature is not consistent with its being a good species, while such scarcity could be expected if it was a rare morph or product of rare hybridization (see Areta 2008, Areta et al. 2011).

Vocalizations have played an important role in illuminating taxonomic dilemmas posed by the finding of new and distinctive plumages of capuchinos, especially since capuchinos do not mimic (Areta 2008, Areta et al. 2011, Repenning et al. 2010b). Geographic variation in the vocalizations of *S. hypoxantha* comprises five regiolects (lowland Bolivia, Entre Ríos, Formosa, Corrientes, and southeast Brazil) (Areta and Repenning 2011), and “uruguaya” has been found within the last three and recorded in Corrientes and Brazil. In all available recordings, “uruguaya” vocalized like the local regiolect of *S. hypoxantha*. We thus predict that “uruguaya” from the province of Formosa should sing identically to the corresponding regiolect of *S. hypoxantha*.

The only capuchino known to breed at El Bagual (Formosa regiolect) is *S. hypoxantha*, which does not migrate in the area, although *S. cinnamomea*, *S. palustris*, *S. ruficollis*, and *S. hypochroma* have been reported passing through during migration (Di Giacomo 2005; pers. obs.). Therefore, in this area there is no regular syntopic or sympatric species with which *S. hypoxantha* might hybridize, giving rise to “uruguaya.” However, since females appear indistinguishable in the field, a remote (and virtually untraceable) chance exists for a female of some species staying to breed and hybridize with *S. hypoxantha*. A large series of *S. hypoxantha* was collected by W. H. Partridge at Estancia Rincón de Luna (Corrientes regiolect, AMNH specimens). Although the locality lies within the breeding range of *S. cinnamomea*, no specimen of *S. cinnamomea* was collected at that time. Thus, again, the presence of “uruguaya” seems attributable to *S. hypoxantha* without need for hybridization to be invoked. Moreover, the single tape-recorded male from Corrientes sang the typical Corrientes regiolect of *S. hypoxantha*, and both members of the pair responded aggressively to playback of *S. hypoxantha*. In the Campos de Cima da Serra in southeastern Brazil, *S. hypoxantha* (southeast Brazil regiolect), *S. melanogaster*, and *S. bouvreuil pileata* are clearly segregated in space and/or

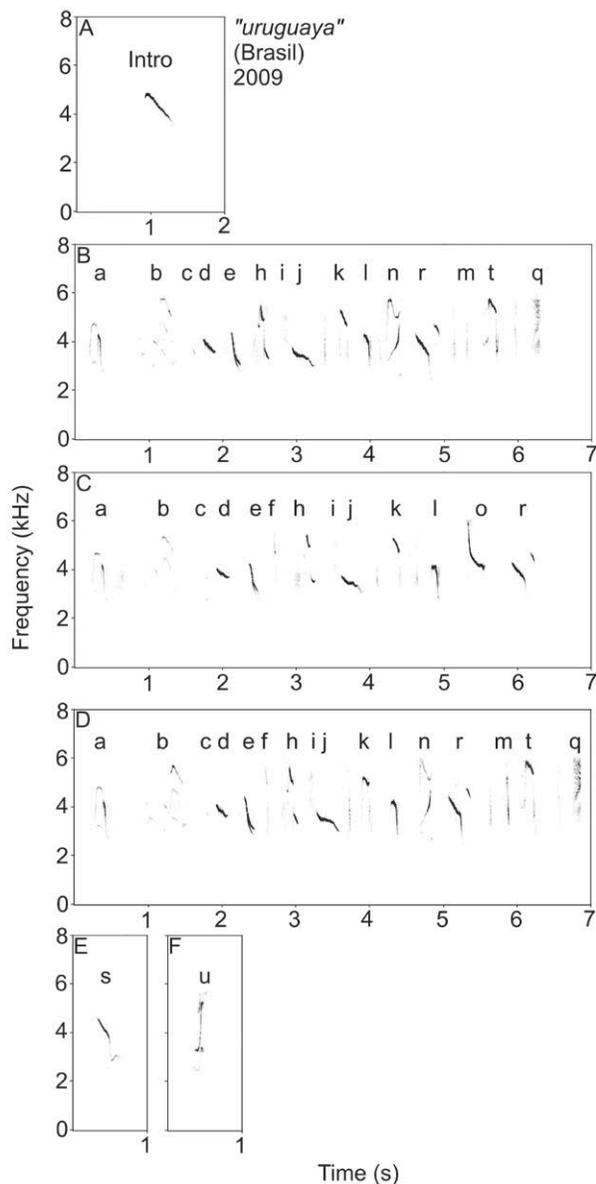


FIGURE 5. Spectrograms of vocalizations of the “uruguaya” form recorded 28 February 2009 at Coxilha Rica, Santa Catarina, Brazil. These vocalizations are indistinguishable from those of the Tawny-bellied Seedeater (*S. hypoxantha*) from the same area (see Areta and Reppenning 2011). (A) Introductory notes, (B–D) song, and (E, F) other notes.

by habitat (Fontana et al. 2009, Reppenning et al. 2010a). The facts that recordings of “uruguaya” available from this area are identical to those of its regiolect of *S. hypoxantha* and that “uruguaya” reacts aggressively to voices of *S. hypoxantha* support its being a morph of *S. hypoxantha*. In southern Entre Ríos (Entre Ríos regiolect) *S. hypoxantha* coexists widely with *S. ruficollis*, *S. palustris*, and *S. cinnamomea*. However, no “uruguaya” is known from this area. Given the rarity of this plumage type, further searches might be necessary to find any, but the lack or scarcity of “uruguaya” in areas where *S.*

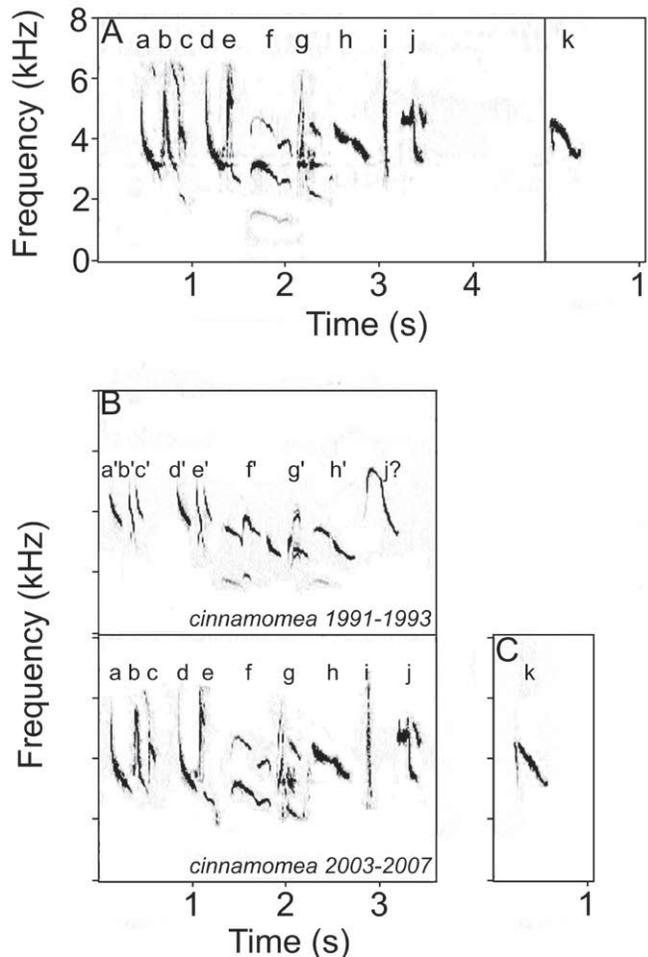


FIGURE 6. Spectrograms of vocalizations of the Chestnut Seedeater (*S. cinnamomea*). (A) Initiation and middle portion of song and call of *S. cinnamomea*, 2003–2007, depicting delimitation of note types, Rincón del Socorro, Corrientes, Argentina; (B) initiation and middle portion of song, 1991–1993, Mercedes, Corrientes, Argentina (above), and 2003–2007, Rincón del Socorro, Corrientes, Argentina (below); (C) Call, 2003–2007, Lorenzo Geyres, Paysandú, Uruguay. An apostrophe denotes inferred homologies; a question mark denotes doubt regarding the homology.

cinnamomea breeds further undermines the hypotheses of hybridization and being a morph of *S. cinnamomea*.

The adult specimen of “uruguaya,” MHNCI 5207, had been identified as *S. cinnamomea* by Eduardo Carrano, but no *S. cinnamomea* is known to have such a light coloration (Lafresnaye 1839, Hellmayr 1904, Narosky 1973, Areta 2008; pers. obs.), and its plumage pattern and coloration agree with those of “uruguaya.” On its label, Lester Short had previously identified AMNH 798521 as a hybrid *S. hypoxantha* × *S. bouvreuil*, but we instead identify it as a young “uruguaya.” We infer that his identification stems from the idea that a hybrid between *S. hypoxantha* and nominate *S. b. bouvreuil* could have the body coloration of *S. hypoxantha* and the back color of *S. b. bouvreuil* (Fig. 2E). However, although *S. bouvreuil* could occur at Estancia Rincón

de Luna, William Partridge collected none there. Moreover, if any *S. bouvreuil* is present in the area, it would be *S. bouvreuil pileata*, the very different gray-backed and white-bellied subspecies of *S. bouvreuil* (Fig. 2E, now considered a separate species by Machado and Silveira [2011] and Areta [2010]); therefore, the allopatry of the putative hybridizing taxa contradicts the hybridization hypothesis put forward by Short on the specimen label. Besides that of “uruguaya,” young males of other collared forms in the group, like *S. “zelichi,”* the “caraguata” form, and *S. cinnamomea*, show the same maturation pattern, namely, a colored collar (including nape and throat) and the remainder of the body creamy and brown, with occasional colored feathers on the back (Areta et al. 2011; pers. obs.). Hence AMNH 798521 is evidently a young “uruguaya” and not a hybrid *S. hypoxantha* × *S. bouvreuil*. Adult males molting out of eclipse plumage seem to follow this same pattern (Areta et al. 2011).

Since we consider the “uruguaya” form to be a morph of *S. hypoxantha*, neither a hybrid nor a valid species, the name “uruguaya” does not require validation under the International Code of Zoological Nomenclature, and we do not recommend the application of a formal name (ICZN 1999, see article 45.6 for more details). We instead propose “uruguaya” as an informal name to enhance communication about this distinctive seedeater (see also Areta et al. 2011 and Repenning et al. 2010b on the similar cases of the “caraguata” and “xumanxu” forms). Detailed descriptions of discrete forms constitute a fundamental element of avian taxonomy, even if they have no standing in the Linnaean hierarchy. The status of many morphs originally described as separate species was established only after careful work. Paradigmatic cases include the dark morph of *Ixobrychus exilis* originally described as *Ardetta neoxena* by Cory (1886) (see Poole et al. 2009) or the morphs of several representatives of the genus *Buteo* originally described as species (see Hellmayr and Conover 1949). Our work with the challenging capuchinos exemplifies the need for ornithologists to be cautious and critical when describing distinct plumages that would have been interpreted as species by default, under the traditional *modus operandi* of taxonomists working in this group (Sclater 1871, Hellmayr 1938, Meyer de Schauensee 1952, Paynter and Storer 1970, Sabel 1990, Ouellet 1992).

EVOLUTIONARY IMPLICATIONS

Our finding of a new tawny variant that seems to be a morph of *S. hypoxantha* recalls the pattern already described for *S. palustris*/*S. “zelichi”* and *S. ruficollis*/*“caraguata,”* in which a common gray-backed form has a rare reddish-backed counterpart (Areta 2008, Areta et al. 2011). Additionally, the black-backed “xumanxu” form is a morph of the localized *S. melanogaster* (Repenning et al. 2010b). However, the strongest parallelism in plumage is that between the pairs *S. hypoxantha*/*“uruguaya”* and *S. hypochroma*/*S. cinnamomea*, with the latter being no more than a chestnut and dark-gray (instead of tawny and light-gray) version of the pattern of the former (Fig. 1). The pairs, however, differ in one outstanding

point: while *S. hypoxantha* and “uruguaya” should be considered morphs of a single species because of their shared vocal repertoire and preferred habitat, *S. hypochroma* and *S. cinnamomea* differ in voice and preferred habitat (and also from *S. hypoxantha*/*“uruguaya”*), so *S. cinnamomea* and *S. hypochroma* must be considered valid species (Areta 2010).

Sporophila hypoxantha varies widely. Vocal, ecological, and plumage variation within *S. hypoxantha* encompasses that found between other recognized species in the capuchino group (Areta and Repenning 2011; this work). Geographically isolated populations that do not differ appreciably in plumage differ in voice and habitat use to a degree equivalent to that between species, while differentiation in plumage (equivalent to that between species) occurs within syntopic populations that do not differ vocally. This study shows that plumage diagnosability can be decoupled from vocal and ecological diagnosability in the capuchinos, providing more evidence for the great lability of plumage features in the capuchinos (Sick 1967, Areta 2009). More importantly, it shows that two non-trivial evolutionary paths can constitute precursors to speciation in the capuchinos. In the first evolutionary path more or less geographically isolated populations diverge in vocalizations and habitat use with little change in plumage (Areta and Repenning 2011), while in the second differentiation in plumage features proceeds without change in vocalizations and habitat use (this work). This young radiation of neotropical seedeaters suggests that differentiation that may trigger speciation can appear both in sympatry and in allopatry: vocal changes seem to need an allopatric phase to develop fully, while plumage changes can occur syntopically. The final outcome of these differing patterns of variation will depend on their interplay through time and space, but they have likely influenced the diversification of the capuchinos.

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APPENDIX 1. List of specimens examined and measured for this study. Abbreviations: American Museum of Natural History (AMNH), New York; Fundación Miguel Lillo (FML), Tucumán, Argentina; Museo Antonio Serrano (MAS), Paraná, Entre Ríos, Argentina; Museo Nacional de Historia Natural y Antropología (MNHNA), Montevideo, Uruguay; Museo Ornitológico de Berisso (MOB), Berisso, Buenos Aires, Argentina; Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul (MCN), Porto Alegre, Brazil; Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul (MCP), Porto Alegre, Brazil; Museu de História Natural Capão da Imbuia (MHNCI), Curitiba, Brazil. No specimens were found in the Museo de La Plata (La Plata, Argentina).

S. hypoxantha: AMNH 127059, 128123, 149721, 149725, 149726, 149728, 320968, 514639, 514640, 514644-514649, 541641-541643, 748892, 748893, 798445-798465, 803348, 811528. IML 2130, 2132. MAS 1992. MCN 2708-2710. MCP 2063, 2559. MHNCI 5014-5016, 5778, 5779.

“Uruguaya”: AMNH 798521, MHNCI 5207.

S. cinnamomea: AMNH 320211, 320653, 320654. MNHNA 6022, 6031, 6108, 6119, 6121. MOB, no number assigned.

APPENDIX 2. Localities at which we recorded habitat use of the “uruguaya” form. Localities are shown in Figure 3. Numbers in brackets, number of individuals or territories per locality.

Argentina, Formosa regiolect [1]: Estancia El Bagual [1]. Corrientes regiolect [2]: Estancia Rincón del Socorro [1], Colonia Pellegrini-Mercedes [1]. Southeast Brazil regiolect [3]: Antiga Estação Ferrea-Bom Jesus [1], Coxilha Rica [2].

APPENDIX 3. Localities of voices of the “uruguaya” form recorded for this study (see Fig. 3). Numbers in brackets, number of individuals per locality; numbers in parentheses, identification number of the individual in JIA database. All recordings by JIA and MR.

Argentina, Corrientes regiolect [1]: Estancia Rincón del Socorro [1] (2). Brazil, Southeast Brazil regiolect [2]: Coxilha Rica [2] (1, 3).