

Unravelling the ecological radiation of the capuchinos: systematics of Dark-throated Seedeater *Sporophila ruficollis* and description of a new dark-collared form

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SUMMARY.—The diverse genus *Sporophila* has a complex systematic history. A new dark-collared form of *Sporophila* seedeater, herein described on the basis of three adult males, resembles male *S. ruficollis* but has a dark nape and rufous back. We informally name the new form 'caraguata' for its preferred habitat. We tested four hypotheses regarding the systematic situation of the 'caraguata' form: valid species, hybrid *S. ruficollis* × *S. cinnamomea*, colour morph of *S. cinnamomea*, and colour morph of *S. ruficollis*. Vocally and ecologically, the 'caraguata' form cannot be diagnosed from *S. ruficollis*. This evidence strongly suggests that *S. 'caraguata'* is a colour morph of *S. ruficollis*, although a hybrid origin is hard to assess and cannot be discarded. *Sporophila ruficollis* differs in preferred habitat, plumage and vocalisations from the rest of the capuchinos, and must be considered a valid species. The pattern of morphological variation exhibited by dark-throated and grey-backed *S. ruficollis* and dark-collared and rufous-backed 'caraguata' is repeated in the white-throated and grey-backed Marsh Seedeater *S. palustris* and white-collared and rufous-backed Entre Ríos Seedeater *S. zelichi*; moreover, the members of each pair are indistinguishable ecologically and vocally. The 'fuzzy' species borders and complicated taxonomy of the *ruficollis* group could stem from an ongoing evolutionary radiation in the capuchinos. This radiation has apparently proceeded with little genetic divergence, simple changes in colour of male plumage, virtually no differences in females, and little morphological change in size and shape, but marked divergence in habitat use and voices of the involved forms.

Sporophila is a large and diverse genus of c.30 species, almost confined to the Neotropics (Ouellet 1992). Because of their short strong bills, they were historically placed with the true finches (Emberizini). However, recent morphological and molecular studies have revealed that they are allied to tanagers (Thraupini) in the tanager-finches group, and their short strong bills are a convergence attained for eating seeds (Clark 1986, Sibley & Ahlquist 1990, Klicka *et al.* 2000, Lijtmaer *et al.* 2004).

Classification of the genus *Sporophila* has been difficult at all levels, from family placement of the genus to colour morph status of several forms. Most revisions and systematic evaluations have relied heavily on plumage characters, making little use of natural history data (Sclater 1871, Hellmayr 1938, Meyer de Schauensee 1952, Olson 1981, Restall 2002, Stiles 2004). Studies of systematics have also largely ignored vocalisations, although these are among the most useful characters for resolving such riddles (Schwartz 1975, Areta 2008).

Systematics have been particularly confusing for the Phyrromelanae, a group originally defined by Bonaparte (1850) to include all of the essentially rufous and black / grey *Spermophilae*, which includes among other taxa those we now recognize as capuchinos:

the 'coloured-cheeked capuchinos' Dark-throated Seedeater *S. ruficollis*, Rufous-rumped Seedeater *S. hypochroma*, Chestnut Seedeater *S. cinnamomea*, Marsh Seedeater *S. palustris*, Entre Ríos Seedeater *S. zelichi*, Tawny-bellied Seedeater *S. hypoxantha*, Black-and-tawny Seedeater *S. nigrorufa*, Capped Seedeater *S. bouvreuil*, and the 'grey-cheeked capuchinos' Ruddy-breasted Seedeater *S. minuta*, Chestnut-bellied Seedeater *S. castaneiventris* and Black-bellied Seedeater *S. melanogaster* (Sick 1997, Lijtmaer *et al.* 2004). Despite the paucity of data, a number of different systematic treatments have been proposed for the *ruficollis* group, i.e. *S. ruficollis* to *S. hypoxantha* as defined above (Sclater 1871, Hellmayr 1904, 1938, Meyer de Schauensee 1952, 1966, 1970, Short 1969, 1975, Paynter & Storer 1970, Narosky & Yzurieta 1987, de la Peña 1989, Ridgely & Tudor 1989, Ouellet 1992, Pearman & Abadie 1995, Silva 1999, Areta 2008, Remsen *et al.* 2009). For example, *S. hypochroma* has been treated as a species (Short 1969, Paynter & Storer 1970), suggested to be a morph of *S. cinnamomea* (Ridgely & Tudor 1989) or treated as conspecific with *S. castaneiventris* (Meyer de Schauensee 1952). Likewise, *S. palustris* is usually treated as a valid species (Hellmayr 1938, Remsen *et al.* 2009), but it was suggested to be a colour morph of *S. hypoxantha* (Short 1975) and *S. zelichi* was recently shown to be a morph of *S. palustris* or a hybrid (Areta 2008). Moreover, females of most (but not all) capuchinos are essentially indistinguishable (Hellmayr 1938) and genetic analyses have failed to clarify the relationships of the different forms because of very shallow and inconsistent differences, especially in the *ruficollis* group (Lijtmaer *et al.* 2004, Kerr *et al.* 2009).

During field work in Entre Ríos province, Argentina, aimed to elucidate the systematics of capuchinos, JIA met many bird-keepers who mentioned a form 'identical to *S. zelichi* but with a black instead of white collar' (Figs. 1–2). Dr M. Zelich, the collector of the type specimens of *S. zelichi*, had been aware of this dark-collared form since at least 1969 and had collected two males (M. Zelich pers. comm.; Graham-Yool 2003). These specimens were loaned to S. Narosky, together with the types of the soon to be described *S. zelichi* (Narosky 1977). Despite this, Narosky (1977) did not mention the dark-collared specimens. The whereabouts of these specimens are uncertain, since they were either reported lost by S. Narosky prior to his description of *S. zelichi* (M. Zelich pers. comm.), or returned to Dr M. Zelich (S. Narosky pers. comm.). The illustration as well as the description erroneously assigned to *S. ruficollis* by Armani (1985) agree well with this overlooked diagnostic plumage; thus, the first published reference to the dark-collared form has not been recognised until now. Pearman & Abadie's (1995) comment that an 'as yet undescribed, *Sporophila* form has been observed twice in south-east Entre Ríos province' also refers to this form (M. Pearman *in litt.* 2007). We observed a presumed subadult male of this form in Corrientes province in Argentina and continued our quest among bird-keepers until, in January and March 2006, we found some that had trapped the bird in the wild. Because unnamed objects are more difficult to reference, we propose the informal name 'caraguata' for this dark-collared form for its preferred habitat of stands of *Eryngium horridum* (Apiaceae) known locally as 'caraguatá'. We use quotation marks to denote that this is neither a subspecies nor a species but at the same time recognise it as a morphologically diagnosable form of seedeater.

The unexpected existence of this diagnostic seedeater opens a door to understanding the radiation of Neotropical seedeaters. Here we (1) describe the new 'caraguata' form of *Sporophila ruficollis*, (2) evaluate four hypotheses regarding its taxonomic status based mainly on comparisons of vocalisations and habitat use with *S. ruficollis* and *S. cinnamomea*, (3) discuss the systematics of *S. ruficollis*, and (4) set the discoveries in perspective within the capuchinos clade by discussing the apparently radiating nature of diversification in the capuchinos and the systematic challenges that arise from these.

Methods

We searched for capuchinos during four breeding seasons between October 2003 and March 2007. Sampling effort totaled 70 days at 26 locations: one day at one location in Buenos Aires (Argentina), 33 days at 11 locations in Entre Ríos (Argentina), 28 days at seven locations in Corrientes (Argentina), three days at two locations in Santa Fé (Argentina), three days at two locations in Paysandú (Uruguay) and three days at three locations in Rocha (Uruguay) (Fig. 3).

We recorded vocalisations using a directional microphone (Sennheiser ME-67) with a Rycote 6 Kit (shock-mount, windshield and windjammer) and a tape-recorder (Marantz PMD-222). Spectrograms were prepared using Syrinx 2.1 (J. Burt, www.syrinxpc.com). Additional recordings were provided by other observers (see Appendix 1). All recordings by JIA are archived at the Macaulay Library of Natural Sounds (Cornell Lab of Ornithology, Ithaca, NY).

The songs of capuchinos include many different, non-repetitive and morphologically complex notes. To compare vocalisations, we first characterised notes which, based on 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 forms.

To characterise habitat use, we assigned each territorial bird to one of four broad habitat categories: (1) caraguatal-cardal, (2) undulating grassland, (3) depressed Pampas grasslands, and (4) annual crops. Caraguatal-cardal is dry grassland on generally level ground with large stands of *Eryngium horridum*, locally known as 'caraguatá' and naturalised thistles (*Carduus* spp.), isolated *Bacharis* spp. shrubs, and occasional *Acacia caven* and *Prosopis affinis* trees. Undulating grassland included upland grasslands on the ridges, valleys and slopes of the Mesopotamian grasslands of Entre Ríos and Corrientes, and close to the Uruguay River in Paysandú. Typical features include rocky outcrops, sandy soils, diverse grasses (e.g., *Paspalum*, *Bromus*, *Piptochaetium*), and occasionally Yatay palms (*Butia yatay*). Depressed Pampas grasslands comprised *Paspalum quadrifarium* and *Spartina densiflora* grassland with occasional *Eryngium* sp. growing on salty soils, in Buenos Aires province. Annual crop habitats were large-scale annual crops, including 'soy' *Glycine max*, 'rice' *Oryza sativa* and 'corn' *Zea mays*, and were present throughout. These habitats are widespread at the geographical scale, and they might co-exist in a mosaic at a single locality or in a reduced geographic area (i.e., the habitats might inter-digitate at the same locality). Although our broad habitat categories may mask subtle habitat segregation at a finer scale, they were designed to apply over a wide area where more detailed descriptions would have precluded the discovery of any habitat-use pattern because many features unique to each site would have masked overall similarities (see sampling localities in Appendix 2).

Because individuals were not marked, we included only data from territorial males that were spatially or temporally segregated to avoid pseudo-replication. For areas visited more than once, we included only one record per territory. We considered each contact to be an independent sample appropriate to evaluate habitat preference, by comparing frequency of occurrence of each form in each habitat. Preferred habitat was defined as that where we found at least 65% of territorial males. Habitat overlap was calculated as the proportion of encounters where two or more species shared a habitat.

We studied plumages and measured bill length (exposed culmen), wing chord, tail length and tarsus length of 67 *S. ruficollis*, nine *S. cinnamomea* and one 'caraguata' from specimens held at the American Museum of Natural History (AMNH, New York), Fundación Miguel Lillo (FML, Tucumán, Argentina), Museo Antonio Serrano (MAS,

Paraná, Entre Ríos, Argentina), Museo Ornitológico de Berisso (Berisso, Buenos Aires, Argentina), Museo de La Plata (MLP, La Plata, Argentina) and Museo Nacional de Historia Natural (MNHN, Montevideo, Uruguay) (Appendix 3). A second ‘caraguata’ was measured as a live specimen held at CICyTTP-CONICET, Diamante, Argentina. Means for all measurements were compared statistically using two-tailed student’s t-test ($\alpha=0.05$).

Systematic hypotheses.—Following Areta (2008), we considered four hypotheses regarding the possible specific validity, hybrid origin, or morph condition of the ‘caraguata’ form (Table 1). These hypotheses stem from the nature of its plumage, apparently intermediate between that of *S. cinnamomea* and *S. ruficollis* (see below), and so here we focus our hypothetical framework on comparisons between these forms, although they can easily be extrapolated to any other set of forms in the group (see Areta 2008, 2010). To avoid subjective preference for any systematic hypothesis, we used the method of multiple working hypotheses (Chamberlin 1965). We deduced predictions for each hypothesis based on the Recognition Species Concept (Paterson 1985), whereby any bird species must have a preferred or normal habitat and a Specific Mate Recognition System (SMRS) that ensures successful reproductive encounters between members of a species (Paterson 1980, 1985, Vrba 1995). Habitat-dependent selection acting on SMRS is thus the main force thought to influence speciation, and two closely related valid species should not share the same preferred habitat. We consider vocalisations to be a key element in species-specific recognition (i.e., a crucial part of SMRS). See Slabekoorn & Smith (2002) for a review of habitat-dependent divergence in vocalisations and speciation. We used the Recognition Species Concept (Paterson 1985) to evaluate the specific status of capuchinos because this concept clearly delimits species and narrows the meaning of species to a restricted biological phenomenon, permits testing of predictions, and makes the results of our study easily interpretable by researchers endorsing other species concepts. Although many of the >30 *Sporophila* species co-exist in the same habitats, they do not regularly appear to be each other’s closest relatives. However, those species we studied are one another’s closest relatives and do not differ obviously in bill morphology. Differences among these capuchinos occur in male plumage, songs and preferred habitat (Areta 2008, 2010; unpubl. data). Therefore, although voice alone might serve to assess specific status of populations, a strong test of specific identity should test voice and distinctive habitat as key features of any valid species. The four hypotheses that we tested were as follows.

(1) Good species hypothesis (GSH). According to this hypothesis, the ‘caraguata’ form is a valid species based on its diagnostic plumage pattern. If so, we predicted that individuals would have vocalisations and a preferred habitat that differed from those of other closely related species.

TABLE 1
Four alternative hypotheses and predictions that permit for an evaluation of the systematic status of the ‘caraguata’ form. For each prediction, support is indicated by (+), rejection by (-) and inconclusive evidence by (±).

Hypothesis	Predictions regarding ‘caraguata’	
	Vocalisations	Preferred habitat
(1) Good species hypothesis	Unique (-)	Unique (-)
(2) Hybridisation hypothesis	Intermediate between <i>S. ruficollis</i> and <i>S. cinnamomea</i> (-) or identical to <i>S. ruficollis</i> or <i>S. cinnamomea</i> (±)	Shared by both <i>S. ruficollis</i> and <i>S. cinnamomea</i> (±, -)
(3) Colour morph hypothesis I	As <i>S. cinnamomea</i> (-)	As <i>S. cinnamomea</i> (-)
(4) Colour morph hypothesis II	As <i>S. ruficollis</i> (+)	As <i>S. ruficollis</i> (+)

(2) Hybridisation hypothesis (HH). This hypothesis considers the 'caraguata' form to be a hybrid between *S. ruficollis* and *S. cinnamomea*, based on the assumption that the rufous back and dark collar of 'caraguata' might originate through hybridisation between the chestnut-bodied *S. cinnamomea* and dark-throated *S. ruficollis*. If true, we predicted that the songs of 'caraguata' would either be intermediate between *S. ruficollis* and *S. cinnamomea* (if songs are genetically determined) or identical to the paternal form (*S. ruficollis* or *S. cinnamomea*, if songs are learned). This hypothesis predicts that the habitat of 'caraguata' would be shared by both parental forms (*S. ruficollis* and *S. cinnamomea*).

(3) Colour morph hypothesis I (CMH I). This hypothesis considers the 'caraguata' form to be a colour morph of *S. cinnamomea*, because the two forms have the back and belly concolorous (both are chestnut in *cinnamomea* but rufous in 'caraguata'). If true, we predicted that 'caraguata' would have songs and preferred habitats like those of *S. cinnamomea*.

(4) Colour morph hypothesis II (CMH II). This hypothesis considers the 'caraguata' form to be a colour morph of *S. ruficollis*, since both have a dark throat and rufous belly. If true, 'caraguata' should have songs and preferred habitats like those of *S. ruficollis*.

Female capuchinos in the *ruficollis* group are indistinguishable by plumage to human observers and their vocal repertoire is usually limited to calls and soft chatters (pers. obs.). Thus, we used male songs and habitat to test all hypotheses. Distribution patterns and relative abundance were also used to assess their validity. Plumage was marginally used to test hypotheses, because plumages constitute the starting point to propose the different hypotheses and similar patterns of variation occur within and between species in the group (Areta 2010), reducing their usefulness to assess species limits in capuchinos.

Results

Description of the 'caraguata' form. Males.—Identical to male *S. zelichi* but black replaces the white throat and nuchal collar (Fig. 1). It is also very similar to *S. ruficollis* but the black nape and rufous back replace the grey nape and back of *S. ruficollis* (Fig. 2). Thus, in 'caraguata' the cap is grey, the throat and nuchal collar black, the rump, back and ventral patches rufous-chestnut and the wings and tail black. The black remiges show the typical white speculum of all capuchinos (Figs. 1–2).

The following descriptions are based on three males. Individual 1 is deposited at the Museo de La Plata (MLP-14044) and individuals 2 and 3 remain alive at the CICyTTP-CONICET for ongoing studies of moult sequence and plumage maturation.

Individual 1 (MLP-14044): forehead and crown lead grey. Nape and hindneck black, joining black of lores, ear-coverts, chin, throat, neck, and breast to the midline. Rufous-chestnut back, rump and abdomen from mid breast to belly and undertail-coverts. Greyish uppertail-coverts with buffy fringes. Blackish primaries with paler and silky underside. White speculum visible on folded wing and extends over base and centre of all remiges, but not on two outermost primaries and two innermost tertials. Buff fringes to greater wing-coverts and secondaries. Blackish upperwing-coverts fringed buff. White underwing-coverts with some chestnut feathers intermixed. Rectrices dorsally blackish, somewhat paler and silky on underside with buff-coloured tips visible above and below. Bill almost entirely black with a notably paler base to mandible. Iris dark brown. Grey tarsus. Captured in the vicinity of Ibicuy (Estación Holt), dpto. Islas del Ibicuy, Entre Ríos, Argentina (59°09'W, 33°44'S; Fig. 3).

Individual 2 (CICyTTP-CONICET): forehead and crown like individual 1, but with some dark rufous-chestnut feathers in crown. The nape marks ill-defined transition between grey crown and a narrow black collar extending and joining black lores, ear-coverts, chin, throat, neck and upper breast. Dark rufous-chestnut back, rump and abdomen from upper breast



Figure 1. Two *Sporophila* males of the dark-collared 'caraguata' form, perching in a caraguatá *Eryngium horridum* plant (Aldo Chiappe)

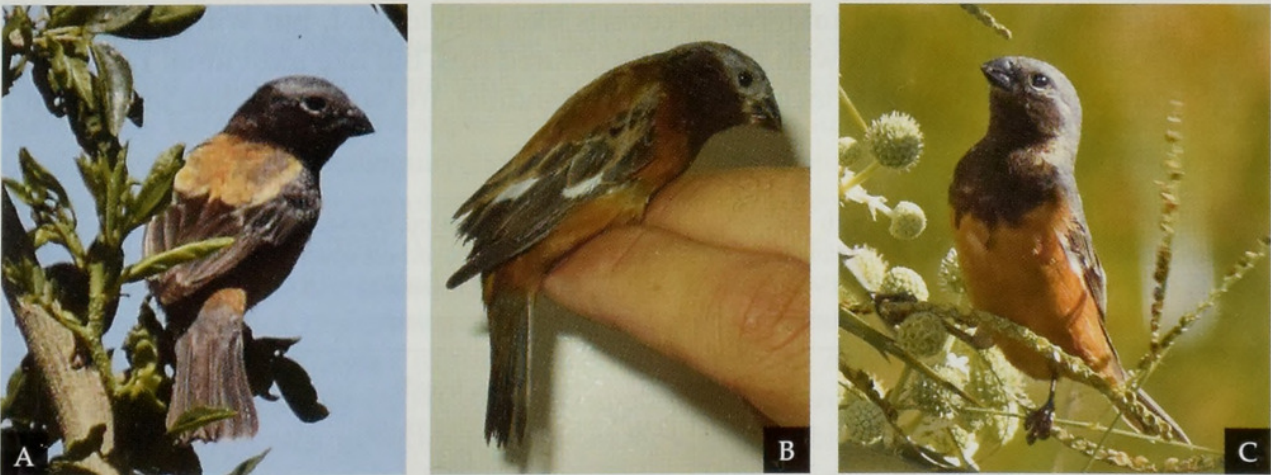
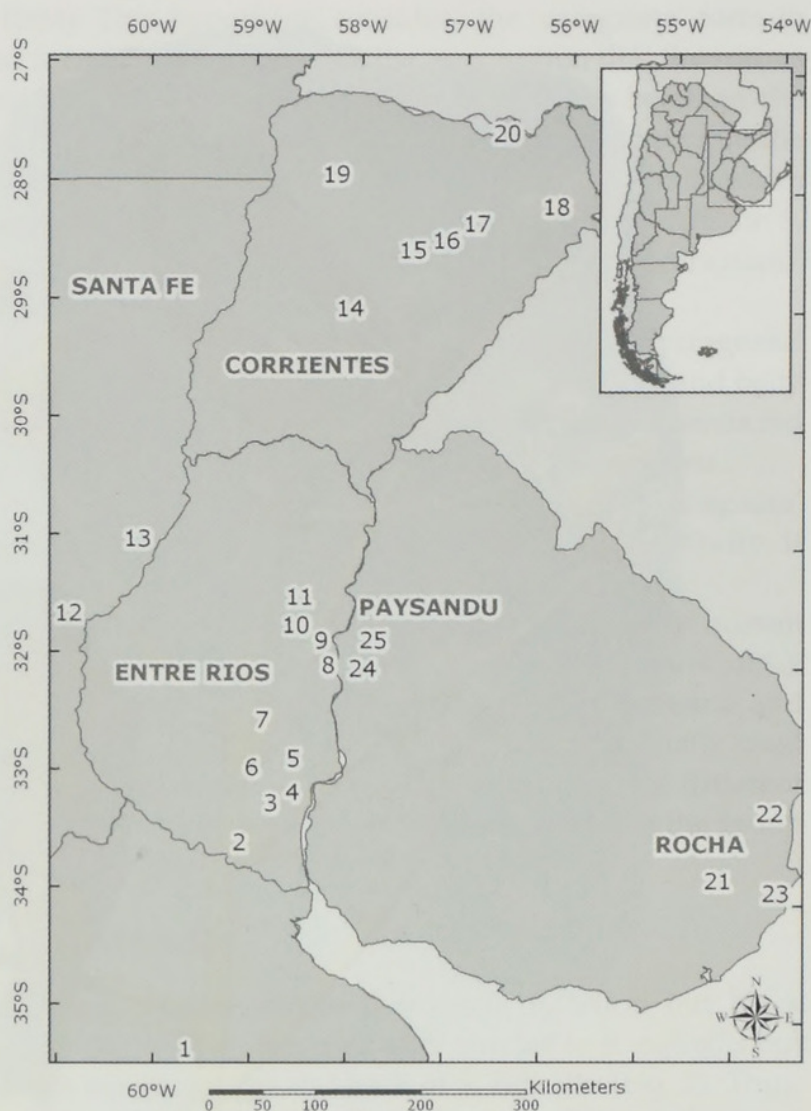


Figure 2. Comparison between the dark-collared 'caraguata' form and Dark-throated Seedeater *Sporophila ruficollis*. (A) Adult male 'caraguata' from Perdices, Entre Ríos Argentina (J. La Grotteria). (B) Adult male 'caraguata' from Las Piedras, Entre Ríos, Argentina (individual 2, see description) (J. I. Areta). (C) Adult male *S. ruficollis* from Mercedes, Corrientes, Argentina (C. Figuerero). Note the distinct black collar and rufous back of 'caraguata' vs. the black throat and grey nape and back of *S. ruficollis*.

Figure 3. Location of sites visited during this study. ARGENTINA. Buenos Aires province: 1. Saladillo (35°30'S, 59°56'W). Entre Ríos province: 2. Ibicuy (33°44'S, 59°09'W), 3. Arroyo Ñancay (33°23'S, 58°44'W) / Perdices (33°18'S, 58°42'W), 4. Estancia La Marita (33°20'S, 58°35'W), 5. Gualaguaychú (33°00'S, 58°30'W) / Las Piedras (32°53'S, 58°33'W), 6. Larroque (33°02'S, 59°00'W), 7. Urdinarrain (32°41'S, 58°53'W), 8. Puerto Liebig and Arroyo Caraballo (32°09'S, 58°11'W), 9. Parque Nacional El Palmar (31°55'S, 58°18'W), 10. Arroyo Baru (31°52'S, 58°27'W), 11. San Salvador (31°37'S, 58°30'W). Santa Fé province: 12. Sauce Viejo (31°46'S, 60°50'W), 13. Campo del Medio (31°08'S, 60°08'W). Corrientes province: 14. Mercedes (29°10'S, 58°05'W), 15. Estancia Rincón del Socorro (28°32'S, 57°10'W), 16. Colonia Pellegrini (28°35'S, 57°10'W), 17. Cambá Trapo (28°27'S, 56°51'W), 18. Cuenca del río Aguapey (28°36'S, 56°56'W), 19. Estancia San Juan Poriahú (27°42'S, 57°11'W) / Parque Nacional Mburucuyá (28°00'S, 58°05'W), 20. Rincón Santa María (27°30'S, 56°35'W). URUGUAY. Rocha Department: 21. Bañados de la India Muerta (33°45'S, 53°50'W), 22. Cebollatí (33°15'S, 53°38'W), 23. Laguna Negra (34°00'S, 53°40'W). Paysandú Department: 24. Lorenzo Geyres, Quebracho (32°04'S, 57°55'W), 25. Queguayar (32°00'S, 57°50'W).



to belly and undertail-coverts; some feathers tinged blackish close to nape impart a blurry streaking. Uppertail-coverts, primaries, speculum, greater wing-coverts and secondaries like individual 1. Upper- and underwing-coverts like individual 1, but without chestnut. Rectrices like individual 1, but with paler buff-coloured tips. Bill like individual 1, but with some horn-coloured markings, including base to mandible. Iris and tarsus like individual 1

TABLE 2

Bill length, wing chord, tail length and tarsus length of Dark-throated Seedeater *Sporophila ruficollis*, Chestnut Seedeater *Sporophila cinnamomea* and the 'caraguata' form based on specimens listed in Appendix 3. Values (in mm) as mean \pm SD (n = sample size) [range] for *S. cinnamomea* and *S. ruficollis*. Individual measurements are given for two 'caraguata'.

	Bill length	Wing chord	Tail length	Tarsus length
<i>S. ruficollis</i>	8.15 \pm 0.11 (56) [7.65–8.75]	53.17 \pm 1.19 (67) [50–55]	38.37 \pm 1.78 (58) [35.0–41.5]	14.03 \pm 0.65 (64) [12.5–15.0]
<i>S. cinnamomea</i>	8.42 \pm 0.44 (9) [7.50–9.05]	52.82 \pm 1.37 (9) [50.95–54.45]	37.25 \pm 0.87 (4) (36–38)	13.65 \pm 0.73 (9) (12.60–14.35)
'caraguata' (1)	8.26	52.5	36.5	14.75
'caraguata' (2)	8.68	53.0	38.5	14.41

(Fig. 2). Captured 13 km north-west of Gualeguaychú at Las Piedras, dpto. Gualeguaychú, Entre Ríos, Argentina (58°33'W, 32°53'S; Fig. 3).

Individual 3 (CICYTTP-CONICET): very similar to individual 1, but differs in broader dark nuchal collar and paler ventral coloration. Captured on the outskirts of Gualeguaychú, dpto. Gualeguaychú, Entre Ríos, Argentina (58°30'W, 33°00'S; Fig. 3).

Individuals 1 and 3 differ from individual 2 mostly in being paler rufous-chestnut, lacking chestnut feathers in the crown, having a broader and better-defined black collar, a neat back without blurry streaking and a black throat extending to the mid breast.

Measurements of 'caraguata' males are indistinguishable from those of *S. ruficollis* and *S. cinnamomea* (Table 2). Two-tailed t-tests showed that bill length was marginally different between *S. ruficollis* and *S. cinnamomea* ($t(63)=2.08$, $p=0.04$) while wing-chord ($t(74)=1.99$, $p=0.42$), tail length ($t(60)=2$, $p=0.22$) and tarsus length ($t(70)=1.67$, $p=0.11$) did not differ significantly (Table 2).

Subadult male.—A presumed young male was found on 22 November 2002 at Estancia San Juan Poriahú, dpto. San Miguel, Corrientes, Argentina (57°11'W, 27°42'S, Fig. 3). Its plumage matched that expected of a young male moulting to adult plumage or a male entering or coming out of 'eclipse' plumage: plain grey crown, black lores, ear-coverts, chin, throat, breast and neck. Back, rump and abdomen pale buffy-brown, similar to females, but with a small patch of chestnut-rufous on the body-sides. Dark wings and tail fringed grey and brown as in adults. The bird did not vocalise. A bird in identical plumage was photographed by J. Spinuzza at Arroyo Ayú-í, Corrientes, Argentina, in December 2006, and birds presumably similar to this were observed with *S. ruficollis* at Iberá Marshes, Corrientes, during spring and summer 2007 / 08 by A. Ocampo (Chebez 2009).

All the above records from Corrientes are tentatively attributed to the 'caraguata' form: since no adults were recorded from these areas, we consider these identifications provisional pending further study.

A male illustrated and described in Armani (1985) as *S. ruficollis* has a complete black collar, rufous rump and belly, and a browner back, suggesting that it was moulting into its breeding, or first adult plumage, or abandoning 'eclipse' plumage. We contest Armani's identification, since his bird is clearly a male 'caraguata' and not *S. ruficollis*.

Females.—Although apparently never collected or trapped (R. Tato pers. comm.), female plumages are doubtless indistinguishable in the field from those of other females of the *ruficollis* group.

Distribution and abundance.—The 'caraguata' form is certainly known from six localities in Entre Ríos and possibly from three localities in Corrientes, all in Argentina (Fig. 3). Adult males from Entre Ríos were trapped at Las Piedras (dpto. Gualeguaychú), on the outskirts of Gualeguaychú (dpto. Gualeguaychú), at Puerto Liebig (dpto. Colón) and Ibicuy (dpto. Islas del Ibicuy). There is also a photographic record from Perdices (dpto. Gualeguaychú) (Fig. 2), and a reliable sighting from Arroyo Nancay (dpto. Islas del Ibicuy) (D. Blanco *in litt.* 2006). The 'caraguata' male illustrated by Armani (1985) is of unknown provenance. Observations of possible subadult males from Corrientes come from Estancia San Juan Poriahú (dpto. San Miguel), Arroyo Ayú-í (dpto. Mercedes) and Iberá marshes (dpto. Mercedes). The 'caraguata' form possibly also occurs in Uruguay (J. C. Mazulla *in litt.* 2006).

Sporophila ruficollis is widespread. It breeds, in suitable habitat, in northern lowland Argentina, Paraguay, lowland Bolivia, western Uruguay and southern Brazil (Sick 1997, Mazar Barnett & Pearman 2001, Azpiroz 2003, Hennessey *et al.* 2003, Guyrá Paraguay 2004; pers. obs.). *Sporophila cinnamomea* has a restricted breeding range, in eastern Argentina, southern Brazil, and eastern and western Uruguay (Sick 1997, Mazar Barnett & Pearman 2001, Azpiroz 2003). Both *S. ruficollis* and *S. cinnamomea* are long-distance migrants and

stem-gleaning specialists (Silva 1999; pers. obs.). At least some *S. ruficollis* and *S. cinnamomea* migrate to the Cerrado of Brazil (Silva 1999, pers. obs.). The 'caraguata' form is migratory, with records spanning November–February in eastern Argentina. Its non-breeding grounds are unknown, but it probably winters together with *S. ruficollis* (see Discussion).

The 'caraguata' form exists in very small numbers in nature: while we only encountered a single male in subadult plumage in the field, a similar search effort produced >200 *S. ruficollis* males and >80 *S. cinnamomea* males.

Habitat.—Dr M. Zelich and ten bird-keepers from Entre Ríos reported capturing at least 15 individuals of this form. In all instances for which precise information is available, territorial males of the 'caraguata' form were caught in habitat typical of *S. ruficollis*: caraguatal-cardal dry grassland ($n=12$, 100%). The adult male from Perdices was in dry grassland with bushes in an agricultural area where several *S. ruficollis* had been present some days before. The sighting from Arroyo Ñancay involved a mixed-species flock of 'caraguata', *S. ruficollis* and Double-collared Seedeater *S. caerulescens* in grassland of *Panicum cf. bergii* (D. Blanco *in litt.* 2006). The subadult 'caraguata' from San Juan Poriahú was feeding in flooded grassland along with *S. bouvreuil pileata*, but only 50 m from a large area of caraguatal-cardal, where only *S. ruficollis* was present and abundant. Based on its passive behaviour and lack of vocalisations this subadult-plumaged bird was apparently not holding territory, but merely feeding gregariously like most capuchinos (see Discussion). We found 110 territorial males of *S. ruficollis*: 82 (74.5%) in caraguatal-cardal, just eight (7.3%) in undulating grasslands, 12 (10.9%) in depressed Pampas grasslands at the southernmost site and eight (7.3%) in annual crops. We found 34 territorial males of *S. cinnamomea*: 25 (73.5%) in undulating grassland, five (14.7%) in marsh or wet grassland and four (11.7%) in cardal-caraguatal.

In synthesis, preferred habitat of 'caraguata' and *S. ruficollis* is caraguatal-cardal, whilst *S. cinnamomea* prefers undulating grassland. All forms occur, in varying numbers, in cardal-caraguatal but in our limited sample 'caraguata' did not occupy undulating grassland like *S. cinnamomea* and *S. ruficollis*.

Vocalisations.—We sound-recorded three 'caraguata' males, 82 *S. ruficollis* males and 24 *S. cinnamomea* males (Appendix 1). Typologically, the capuchinos featured in this study have three main voice types: an introduction, a main song and various calls.

We detected geographic variation in the voice of *S. ruficollis*. This variation can be accommodated in two regiolects ('song variants encompassing extensive subpopulations of a species and all individuals within this large range', Martens 1996: 221): the Mesopotamia regiolect in Argentina and Uruguay, and the Alto Madidi regiolect in Bolivia (Figs. 4–5, Appendix 1; Areta 2010).

In the Mesopotamia regiolect, we identified an introduction and 19 notes in the repertoire of *S. ruficollis* (Fig. 4, Table 3). The introduction of *S. ruficollis* in the Mesopotamia regiolect comprises a variable number of notes (usually 2–4). Typically, the first two notes are flat, with the second slightly higher pitched than the first. If present, the third note is either flat or descending, and a fourth distinctively descending and higher pitched note can be given (Fig. 4A–B). Variation in the number of introductory notes occurs both inter- and intra-individually. The introduction can be given alone several times or as an introduction to the main song.

The typical main song in the Mesopotamia regiolect is a long complex series of variously shaped notes delivered at a leisurely pace (Fig. 4C–E). Depending on the level of excitement, singing males can vary the number of final notes in a series, sometimes even linking complete songs. Although the typical sequence of notes is depicted in Fig. 4, the sequence can be altered to follow no obvious pattern (i.e., apparently random). Such

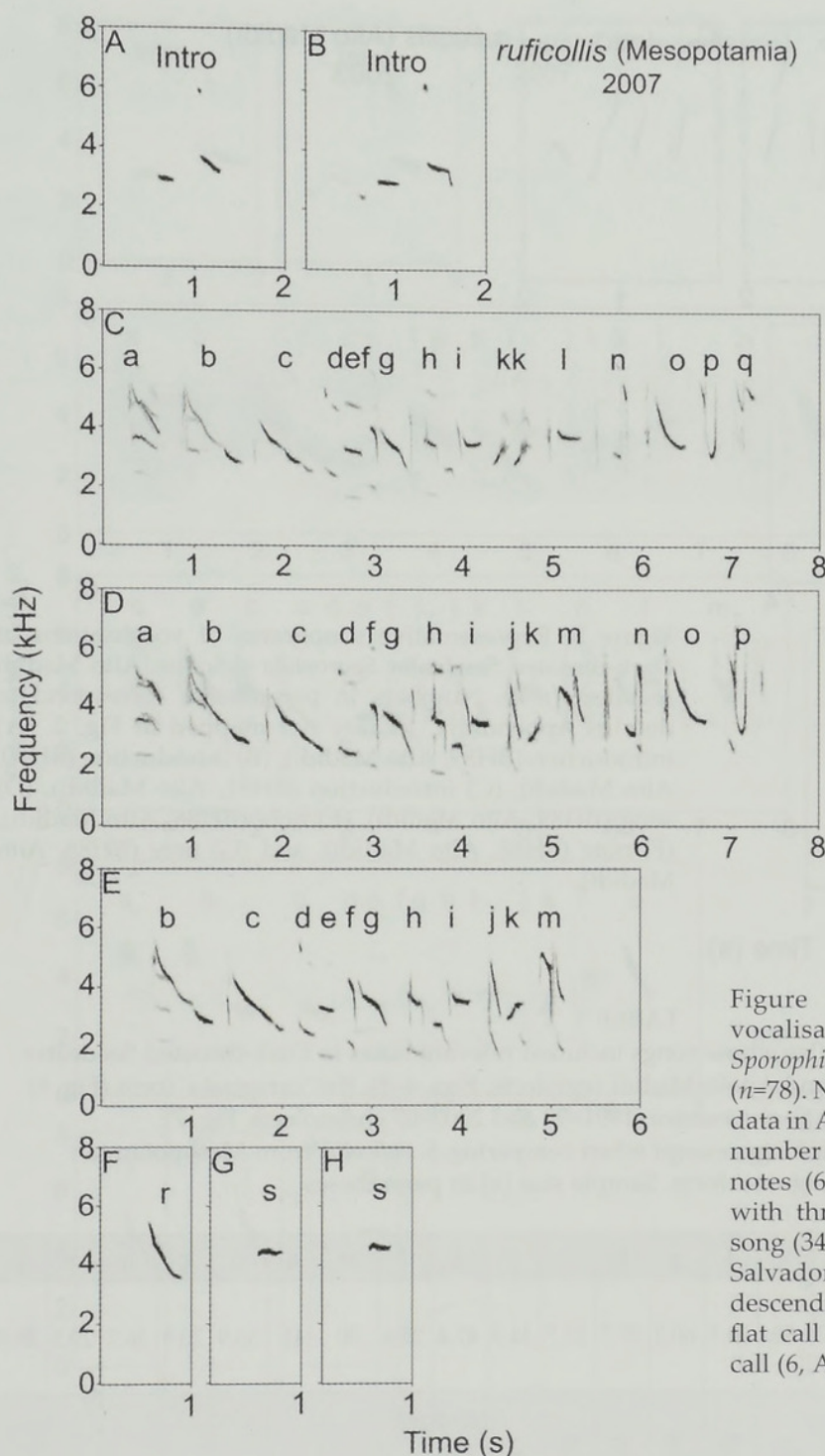


Figure 4. Representative sonograms of vocalisations of Dark-throated Seedeater *Sporophila ruficollis*, Mesopotamia regiolect ($n=78$). Numbers in parentheses correspond to data in Appendix 1, locality name and locality number as in Fig 2. (A) introduction with two notes (6, Arroyo Baru-10), (B) introduction with three notes (34, Gualeguaychú-5), (C) song (34, Gualeguaychú-5), (D) song (11, San Salvador-11), (E) song (6, Arroyo Baru-10), (F) descending call (34, Gualeguaychú-5), (G) flat call (34, Gualeguaychú-5), and (H) flat call (6, Arroyo Baru-10).

variation can occur in successive songs of the same individual. Singing males can also deliver parts of the main song randomly and occasionally perform a song comprising series' of notes lacking any clear pattern. We identified two main calls in the repertoire of *S. ruficollis*: a descending arched call (Fig. 4F) and a flat high-pitched call (Fig. 4G-H).

The Alto Madidi regiolect is based on few data but we identified an introduction and 11 notes in an isolated population of *S. ruficollis* from the Apolo-Madidi savannas, Bolivia. This population shows consistent vocal differences from populations in the lowlands of Argentina and Uruguay (Fig. 5, Table 3).

We did not detect any geographical variation in voices of 'caraguata' from Argentina, with the same note types identified at all localities. The introduction (Fig. 6A-B), full song (Fig. 6C-E) and calls (Fig. 6F-H) conform to the normal individual variation in structure

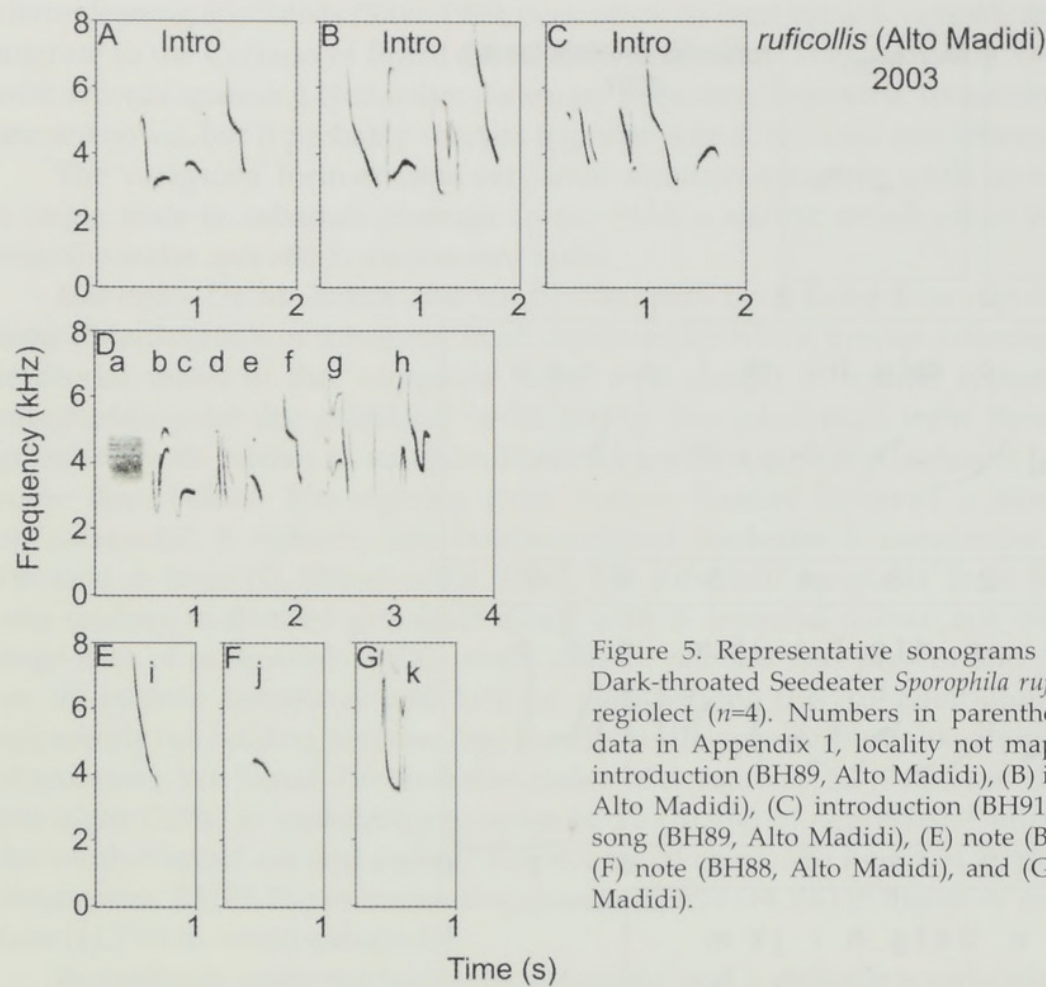


Figure 5. Representative sonograms of vocalisations of Dark-throated Seedeater *Sporophila ruficollis*, Alto Madidi regiolect ($n=4$). Numbers in parentheses correspond to data in Appendix 1, locality not mapped in Fig. 2. (A) introduction (BH89, Alto Madidi), (B) introduction (BH90, Alto Madidi), (C) introduction (BH91, Alto Madidi), (D) song (BH89, Alto Madidi), (E) note (BH88, Alto Madidi), (F) note (BH88, Alto Madidi), and (G) note (BH88, Alto Madidi).

TABLE 3

Note types and % of individual males whose songs included relevant notes in Dark-throated Seedeater *Sporophila ruficollis* (Mesopotamia and Apolo-Madidi regiolects, Figs. 4–5), the ‘caraguata’ form (Fig. 6) and Chestnut Seedeater *S. cinnamomea* (1991–93 and 2003–07 chronolects, Fig. 7).
Note names do not imply homology, except when comparing *S. ruficollis* from Mesopotamia and the ‘caraguata’ form. Sample size (n) in parentheses.

	Intro.	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	q	r	s
<i>S. ruficollis</i> Mesopotamia, 2003–08 (78)	66.7	66.7	65.4	61.5	57.7	59	60.3	60.3	57.7	57.7	44.9	47.4	25.6	50	41	35.9	20.5	16.7	29.5	38.5
<i>S. ruficollis</i> Apolo Madidi, 2003 (4)	75	50	25	25	25	25	50	25	25	25	25	50								
‘caraguata’ Mesopotamia, 2007 (3)	66.7	100	100	100	100	100	100	100	100	100	100	100	100	66.7	66.7	66.7	100	66.7	100	100
<i>S. cinnamomea</i> , 1991–93 (4)		100	100	100	75	75	100	75	75		75									
<i>S. cinnamomea</i> , 2003–07 (20)		65	65	55	65	65	65	65	65	55	65	50								

of the Mesopotamia regiolect of *S. ruficollis* (Fig. 4A–H). Hence, there are no consistent vocal differences between ‘caraguata’ and *S. ruficollis*. Given the conservatism in the basic vocal structure in *S. ruficollis* from the Mesopotamian grasslands ($n=78$), we suggest that

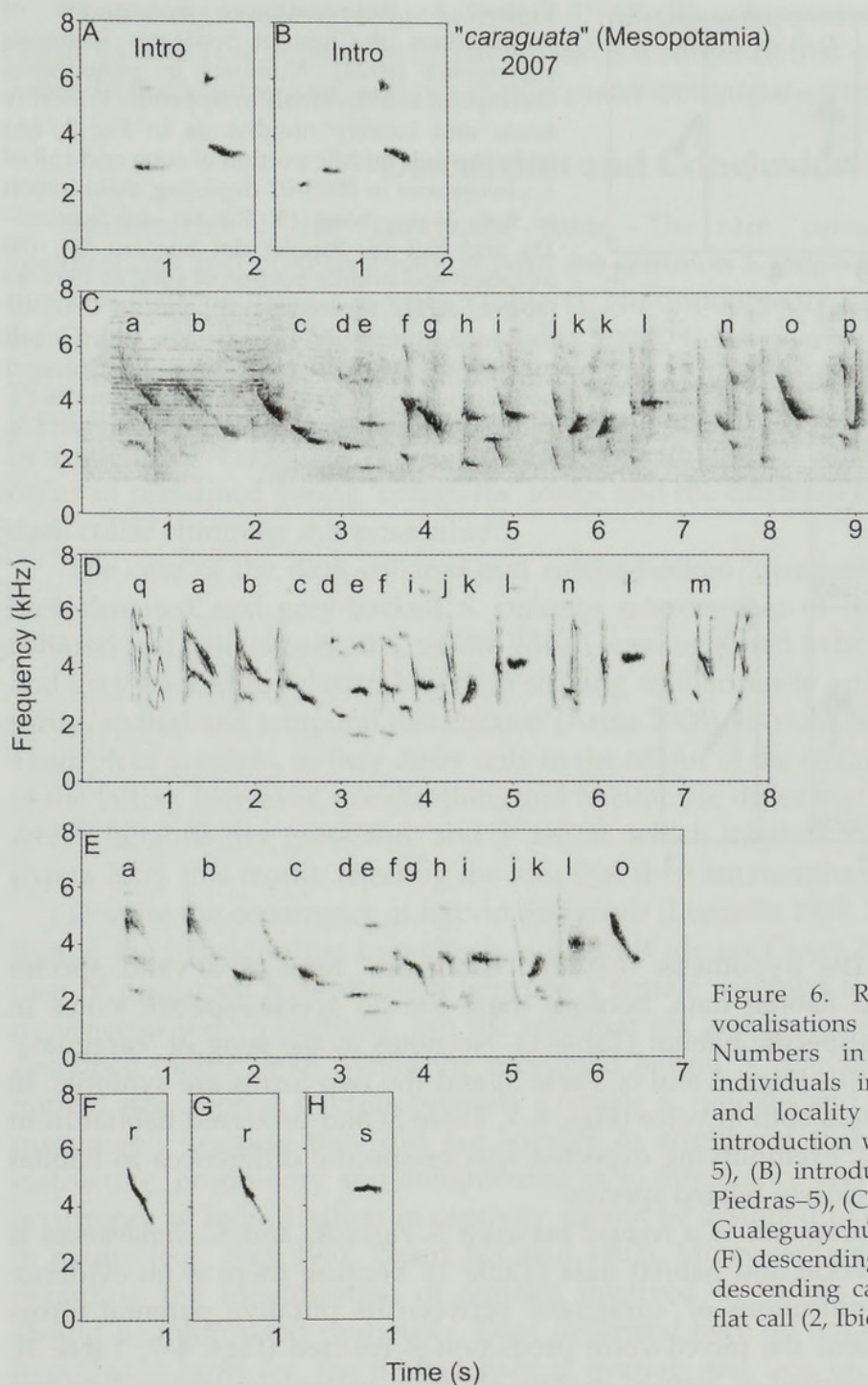


Figure 6. Representative sonograms of vocalisations of the 'caraguata' form ($n=3$). Numbers in parentheses correspond to individuals in Appendix 1, locality name and locality number as in Fig. 2. (A) introduction with two notes (1, Las Piedras-5), (B) introduction with three notes (1, Las Piedras-5), (C) song (2, Ibicuy-2), (D) song (3, Gualaguaychú-5), (E) Song (1, Las Piedras-5), (F) descending call (3, Gualaguaychú-5), (G) descending call (1, Las Piedras-5), and (H) flat call (2, Ibicuy-2).

our recordings of 'caraguata' ($n=3$ individuals) are probably representative of the form in this region. A fourth male 'caraguata' from Perdices (not tape-recorded), responded aggressively to playback of *S. ruficollis* and its song was identical (J. La Grotteria *in litt.* 2010). Trappers reported that all 'caraguata' ($n=12$) were attracted to the voice of *S. ruficollis* and that they ignored voices of species such as *S. palustris* and *S. cinnamomea*, which were also used in trapping attempts.

Main song and calls of *S. cinnamomea* do not resemble those of *S. ruficollis* or 'caraguata' (Figs. 4–7, Table 3). None of the notes in the repertoire of *S. ruficollis* and 'caraguata' was present in the songs of *S. cinnamomea*, for which 11 diagnostic notes were identified (Fig. 7, Table 3). The last segments of the full song of *S. cinnamomea* were seldom recorded and could not be characterised. No geographical variation was detected but old recordings of *S. cinnamomea* differ from modern recordings (*cf.* Areta 2008).

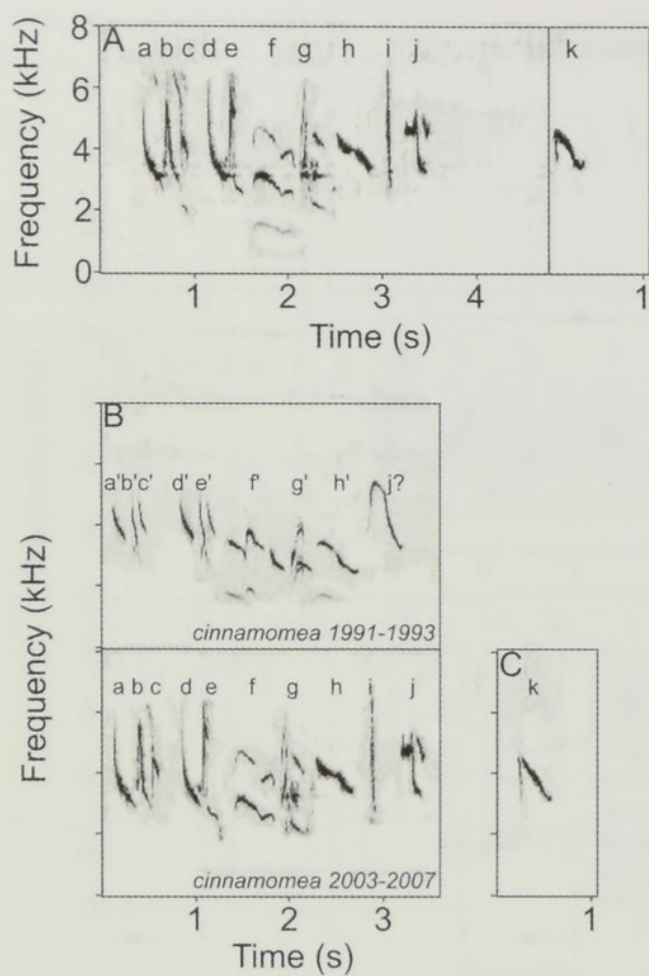


Figure 7. Representative sonograms of vocalisations of Chestnut Seedeater *Sporophila cinnamomea* ($n=24$). Numbers in parentheses correspond to individuals in Appendix 1, locality name and locality number as in Fig 2. (A) initiation and middle portion of song and call of *S. cinnamomea* in 2003–07 depicting delimitation of note types; song (5, Rincón del Socorro–15) and call (5, Rincón del Socorro–15), (B) initiation and middle portion of song in 1991–93 (above, AJ21, Mercedes–14), and in 2003–07 (below, 5, Rincón del Socorro–15), and (C) call in 2003–07 (14, Lorenzo Geyres–24). Inferred homologies are described using apostrophes ('), and interrogation mark denotes doubt regarding homology.

Hypothesis testing.—The hypothesis that the ‘caraguata’ form is a valid species is rejected using song and habitat data, because there are no species-specific notes in their songs and no species-specific habitat (Table 1). No notes in the song of ‘caraguata’ distinguish it from *S. ruficollis* (Figs. 4 and 6, Table 3) and the two forms are syntopic. In contrast, *S. cinnamomea* differs both in voice (Figs. 4–7, Table 3) and preferred habitat from ‘caraguata’ and *S. ruficollis*, exemplifying expected species-specific differences in habitat and vocalisations between closely related species.

The hypothesis that ‘caraguata’ is a hybrid between *S. ruficollis* and *S. cinnamomea* is partially rejected by both vocal and habitat data (Table 1). Because there is no evidence of intermediacy in the vocalisations of ‘caraguata’ between its putative parental forms *S. ruficollis* and *S. cinnamomea*, the mixed-voice prediction is rejected (Figs. 4–7, Table 3). However, if songs were inherited or learned exclusively from males, similarities between songs of *S. ruficollis* and ‘caraguata’ would be expected even if the latter is a hybrid. If ‘caraguata’ is of hybrid origin and songs are learned, evidence suggests that *S. ruficollis* is always the paternal form. Habitat overlap between the proposed parental forms *S. cinnamomea* and *S. ruficollis* is limited, but sufficient to permit hybridisation. However, ‘caraguata’ was never found in the undulating grassland habitat of *S. cinnamomea*. Thus, voice and habitat suggest that male *S. cinnamomea* might not be important in the origin of ‘caraguata’. None of this hypothesis’ predictions was fully supported by our results.

The hypothesis that ‘caraguata’ is a colour morph of *S. cinnamomea* is rejected based on vocal and habitat data (Table 1). The songs of ‘caraguata’ and *S. cinnamomea* differ in note structure, pace and duration (Figs. 6–7, Table 3). Furthermore, there is little habitat overlap between ‘caraguata’ and *S. cinnamomea*, and ‘caraguata’ was never found in the preferred habitat of *S. cinnamomea*.

That 'caraguata' is a colour morph of *S. ruficollis* is supported by vocal and habitat data (Table 1). The note repertoire of 'caraguata' is a subset of that of *S. ruficollis* (Figs. 4 and 6, Table 3). Both 'caraguata' and *S. ruficollis* prefer caraguatal-cardal habitat.

Discussion and Conclusion

Systematics of the 'caraguata' form.—The rare 'caraguata' form coincides in vocalisations and preferred habitat with the common *S. ruficollis*, providing evidence that they are syntopic colour morphs (Table 1). No undoubtedly valid species of *Sporophila* is extremely rare in adequate habitat (Areta 2008). Consequently, we interpret the extreme rarity of 'caraguata' as further undermining the valid species hypothesis. However, rarity is consistent with both the presence of a morph or hybridisation events. Although it might be argued that 'caraguata' represents older individuals of *S. ruficollis*, the presence of a dark collar in presumed young 'caraguata' males and the existence of old *S. ruficollis* without a dark collar eliminate this possibility.

The case of the dark-collared and rufous-backed 'caraguata' form as a morph of the dark-throated and grey-backed *S. ruficollis* mirrors that of the exceedingly rare white-collared and rufous-backed *S. zelichi*, which was suggested to be a morph of white-throated and grey-backed *S. palustris* based on striking similarities in voice, habitat, and patterns of rarity, spatial and temporal distribution (Areta 2008). It could be argued that 'caraguata' is a morph of *S. zelichi*, as they differ only in the colour of the collar (dark in the former, white in the latter). However, vocalisations and habitat use differ markedly between 'caraguata', which inhabits dry grassland, and *S. zelichi*, which inhabits marshes and wet grasslands (Areta 2008, this work), rejecting the idea that they are morphs of the same species.

Despite the occurrence of hybrid *Sporophila* (Lordello 1957, Sick 1963, 1997; pers. obs.), testing the hybridisation hypothesis is difficult (de las Casas 2004, Areta 2008). The only case of presumed hybridisation between a female assigned to *S. ruficollis* and a male *S. cinnamomea* was in captivity, but the resultant sex and plumages of the hybrids were not described (Sabel 1990). While the presumed hybrid *S. ruficollis* × *S. cinnamomea* reached normal size, captive hybrids between a female *S. ruficollis* and a male *S. palustris* did not, presumably because they did not survive to adulthood (Sabel 1990). Although highly instructive, promissory and enlightening as to inheritance and ontogeny of plumage, the occurrence of hybridisation in captivity cannot be assumed to demonstrate its occurrence in nature (e.g., Sick 1962, Grant & Grant 1992). Moreover, given the lack of critical data regarding the identification of females involved in Sabel's (1990) crossings, the data should be interpreted cautiously. Data presented here do not eliminate the hybridisation hypothesis; however, the limited habitat overlap and lack of shared vocal characters of 'caraguata' with *S. cinnamomea* are inconsistent with hybrid origin (Table 1). Our 'caraguata' specimen, live individuals and observations agree in colour intensity with *S. ruficollis*, but never approach the chestnut saturation in male *S. cinnamomea* (see below), providing further evidence against the hybrid hypothesis.

Because *S. ruficollis* is more widespread than *S. cinnamomea*, further testing of the hybridisation hypothesis and colour morph hypothesis II is possible. The hybridisation hypothesis predicts that 'caraguata' should occur only where *S. cinnamomea* is also present (assuming philopatry of hybrids), while colour morph hypothesis II predicts that 'caraguata' could potentially appear anywhere within the range of *S. ruficollis*, independent of the presence of *S. cinnamomea*. Measurements do not differ consistently between *S. ruficollis*, *S. cinnamomea* and 'caraguata', and do not appear useful in elucidating the systematics of the group.

Geographic variation in the vocalisations of *S. ruficollis* was detected in this study, with two widely allopatric regiolects (Mesopotamia and Alto-Madidi), but 'caraguata' was found only within the area of occurrence of the Mesopotamia regiolect, and sings like birds there. Both *S. ruficollis* and presumed 'caraguata' males from Corrientes, Argentina, should be tape-recorded for comparison as their voices might differ from those elsewhere (pers. obs.). The few recordings of the apparently isolated and resident population of *S. ruficollis* in the Apolo-Madidi savannas (Bolivia) exhibit several differences from those from Argentina and Uruguay, and merits further study. Although imitation has been reported for several *Sporophila* not closely related to the capuchinos—Rusty-collared Seedeater *S. collaris* (Moschione 1989; pers. obs.), Grey Seedeater *S. intermedia* (Thomas 1996) and Plumbeous Seedeater *S. plumbea* (Sick 1997; pers. obs.)—we lack evidence of vocal mimicry in any capuchino (JIA unpubl.: $n=230$ individuals of all species in the *ruficollis* group). Moreover, the concerted vocal changes over time in *S. palustris*, and its presumed morph *S. zelichi*, suggest a common mechanism of restriction in vocal learning (Areta 2008). Unfortunately, we lack comparable recordings of *S. ruficollis* and 'caraguata' through time to further test this hypothesis.

Although 'caraguata' would have been considered a species using the traditional colour-based species delimitation criteria in capuchinos, the evidence does not support this (Table 1). The concept of morph (Huxley 1955, Gray & McKinnon 2006) implies that exclusive assortative mating within a species is not strictly dependent upon the presence of a single plumage pattern (i.e., *ruficollis* females would be more attracted to both *ruficollis* and 'caraguata' males over hetero-specific plumages). This underscores the importance of not assuming *prima facie* that diagnosable plumage traits directly represent discrete biological entities. The association of complementary plumage and vocal traits presumably provides key species-specific cues for recognition (Irwin & Price 1999, Price 2007), but the precise mechanisms through which plumage pattern and voices are involved in recognition or the effect of mis-associated male plumage and vocal features on female choice (e.g., a *S. cinnamomea* plumaged male with a *S. ruficollis* voice) have not been explored to date in capuchinos. Finally, if 'caraguata' is a morph product of a rare allele, the commonly traded *S. ruficollis* should be protected to ensure its long-term persistence.

Systematics of *S. ruficollis*.—Because our data are more consistent with the notion that 'caraguata' is a morph of *S. ruficollis*, we now discuss the systematics and taxonomy of *S. ruficollis*. *Sporophila ruficollis* Cabanis, 1851, was described from a young male presumably from Montevideo (Uruguay), based on the manuscript / label name *Fringilla ruficollis* assigned by Lichtenstein to a specimen in Berlin. Sclater (1871) and Sharpe (1888) considered *S. ruficollis* to be a young *S. hypoxantha*. The link between the type of *S. ruficollis* (grey cap, chocolate throat, pale creamy underparts and brownish upperparts) and adult males was only elucidated by Hellmayr (1904, 1938) who subsumed *Spermophila plumbeiceps* Salvadori, 1895, in *S. ruficollis*. Hellmayr (1904, 1938) discussed plumage variation in *S. ruficollis*, while casting doubt on the validity of the type locality, albeit without rationale. However, Lichtenstein (1854: 46) reported a specimen from 'Brasilien' held in Berlin, presumably the type that Hellmayr (1904, 1938) examined. Unfortunately, the type of *S. ruficollis* cannot be found in the Museum Heineanum (Halbserstadt: B. Nicolai *in litt.* 2009) or Museum für Naturkunde (Berlin: S. Frahnert *in litt.* 2009), and appears to be lost.

Our data on *S. ruficollis* based on specimens and field observations agree with those previously published on the great variability in pigment saturation in the species (Hellmayr 1904, 1938, Meyer de Schauensee 1952, 1966). Most important, for taxonomy, are the variations in throat and belly colour. In presumed adult males, the colour of the throat varies from dark rufous to black, while the belly is pale to dark rufous. This suite of variants

occurs in the same habitats in large geographical areas where no other male capuchino is found, supporting its purely individual nature. Our field observations suggest that darker individuals are older males (Hellmayr 1904). However, dark and pale siblings of the same age occur in captivity (R. Tato pers. comm.), suggesting that darker pigmentation is a function of both age and individuality.

Short (1969a: 219) suggested that *S. ruficollis* might be a colour morph of *S. hypoxantha*, and contested that 'Both dark and light throated forms are found side by side in the same wet pampas of Corrientes, and probably elsewhere'. However Hartert & Venturi (1909: 175), stated that *S. ruficollis* nests 'in the little bushes . . . found here and there in the dry and elevated fields', and that *S. hypoxantha* 'nests amidst the short grasses found in areas with marsh ant nests'. Short (1975) added that *S. ruficollis* and *S. palustris* are colour morphs of *S. hypoxantha*, although he noted that field studies were needed to clarify this, and he found habitat of parental forms and presumed hybrids an important taxonomic indicator (Short 1969b: 85). *S. ruficollis* (this work) and *S. hypoxantha* (Hartert & Venturi 1909, Areta 2010) differ in voice and preferred habitat, whilst differences in habitat, vocalisations and distributions suggest species-level differences for *S. ruficollis* and *S. palustris* (Areta 2008, this work). Thus, there is no support, on natural history grounds, to consider *S. hypoxantha*, *S. ruficollis* and *S. palustris* as colour morphs of the same species (but see below for an alternative polymorphism hypothesis).

Sabel (1990) suggested that *S. zelichi* is a morph of *S. ruficollis*, based on unstated evidence, whilst Lewis (1997) proposed, based on limited mtDNA evidence (cytochrome-*b* 350bp, pair-wise distance 1.3%) that *S. ruficollis* is more closely allied to *S. zelichi* than to other capuchinos, and that they could be 'colour phases' of the same species. The data presented here, together with those of Areta (2008) reject this idea: *S. zelichi* differs in vocalisations and preferred habitat from *S. ruficollis*, aside from their very different plumages. Finally, Armani (1985) illustrated a male 'caraguata' as representative of *S. ruficollis*, which we consider erroneous (see Results).

In sum, our results support treatment of *S. ruficollis* as a valid species, with the inclusion of the rare 'caraguata' form as a colour morph. Because females have to date proved indistinguishable among all species in the *ruficollis* group we cannot evaluate whether there are also female morphs. Until this question is elucidated, *S. ruficollis* should be considered a male-dimorphic species.

Radiating capuchinos?—The lack of genetic structure in the *ruficollis* group (Lijtmaer et al. 2004, Kerr et al. 2009) conflicts with the clear differences in plumage, vocalisations and habitat use (Areta 2008, 2010, this work). This apparent incongruence suggests: (1) recent divergence not yet reflected in the studied genes; or (2) the existence of an ultra-polymorphic species with varying degrees of isolation between different forms in the *ruficollis* group (Areta 2008). Under the second hypothesis, female capuchinos may mate freely with all male forms, erasing any genetic distinctiveness, while the diagnostic features of voice and habitat preference of males could be cultural traits over-imposed on a common gene pool. This hypothesis differs from the simple colour morph hypothesis proposed by Short (1969b, 1975) in which birds merely differ in plumage.

Habitat imprinting could play a crucial role in the generation and maintenance of habitat preferences in birds (Davis & Stamp 2004, Beltman & Haccou 2005) which could result in assortative mating within preferred habitats. In turn, magnitude of ecological divergence can also play an important role in reproductive isolation independent of divergence time between forms (Funk et al. 2006, Nosil et al. 2009). Sick (1967: 309) stated that 'habitat segregation—which prevents the meeting of potential mates—represents, in the case of seedeaters, the most important isolating mechanism'. Given the contrast between the

scant genetic differentiation and the habitat divergence in these forms, habitat segregation through imprinting is thought to play a key role in the evolution of capuchinos (Areta 2010). Two issues are worth mentioning. First, preferred habitats often occur side by side in the Mesopotamian grasslands of Argentina and in Uruguay, permitting potential mixing between males and females of most forms spatially and temporally. Second, capuchinos forage and migrate in mixed-species flocks. These can be misleading when evaluating breeding habitat, because habitat use by mixed flocks does not necessarily correspond to the preferred habitat of breeders and territorial males (pers. obs.). For example, Azara (1802) was confused when he included *S. bouvreuil pileata*, *S. ruficollis*, *S. palustris* and probably even a young *S. cinnamomea* in the 'Pico Grueso Variable'. He collected birds that differed in body-feathers but not in wing pattern in the same flocks, and erroneously considered them a single highly variable species.

Early stages of evolutionary radiations are characterised by 'fuzzy' species borders with frequent hybridisation (Price 2007, Grant & Grant 2008). Capuchinos, especially the *ruficollis* group, might represent a very early evolutionary radiation, with the ecologically differentiated forms capable of hybridising but rarely producing fit hybrids and back crosses. Differentiation presumably occurred with very little genetic divergence, simple changes in colour patches of male plumages, divergence in habitat and voices, but little morphological change in size and shape and virtually no differences among females (Areta 2010). The existence of several new forms of capuchinos in the process of being described will provide data to further test these ideas.

The taxonomic conundrum.—The 'caraguata' form is not a species under the Recognition Species Concept (or the Biological Species Concept and probably also under some versions of the Phylogenetic Species Concept; see Eldredge 1995, Haffer 1997). Although most evidence supports it being a colour morph of *S. ruficollis*, a slight possibility exists that it is a hybrid. Clearly, this situation is conflictive, since traditional taxonomic concepts and methods do not suffice to provide a name or category to accurately describe this situation (Selander 1971, Grant & Grant 2006, 2008).

If we explicitly consider 'caraguata' a morph of *S. ruficollis*, then 'caraguata' is an infra-subspecific name according to the *International code of zoological nomenclature* (ICZN 1999). Names expressly proposed to denote infra-subspecific entities are not available under the rules of the ICZN, are excluded from the species group and not regulated by the ICZN (1999; Art. 45.6). Although the ICZN does not preclude the erection of names for taxa of hybrid origin (Arts. 1.3.3, 17.2 and 23.2), it would be confusing (if 'caraguata' subsequently proves to be a hybrid) to erect a new species name for this peculiar systematic situation.

We have referred to this diagnostic plumage as 'caraguata' or the 'caraguata' form. An alternative would be to employ an informal binomial, i.e. *Sporophila* 'caraguata', to denote its uncertain taxonomy, as used elsewhere in *Sporophila* (Olson 1981). However, our referees argued strongly against this, despite its usefulness to accommodate the situation of both *S. 'zelichi'* and *S. 'caraguata'* (Areta 2008, 2010). We strongly recommend acknowledging the uncertainty regarding hybrid origin by referring to 'caraguata' as either *Sporophila* 'caraguata' or the 'caraguata' form, and suggest caution with the use of alternatives directly acknowledging its morph status as *Sporophila ruficollis* morph 'caraguata' or *Sporophila ruficollis* dark-collared morph.

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APPENDIX 1: recording localities, dates and identification of voices

Localities are shown in Fig. 3. Numbers in [] indicate number of individuals per locality and those in () indicate number assigned to each bird in JIA database. All recordings by JIA except those by AJ = Alvaro Jaramillo, BH = Bennett Hennessey, MP = Mark Pearman, RF = Rosendo Fraga. All recordings of ‘caraguata’ are from birds in captivity.

S. ruficollis [82] **Mesopotamia regiolect** [78]. ARGENTINA. Entre Ríos: Arroyo Baru [8] (4–11), Larroque-Urdinarraín [11] (20–27, 38–40), San Salvador [6] (12–17), Gualaguaychú [5] (33–37), Estancia La Marita [4] (1, 2, 18, 19), Puerto Liebig and Arroyo Caraballo [1] (3). Santa Fé: Sauce Viejo [5] (28–32). Buenos Aires: Saladillo [10] (41–50). URUGUAY. Dpto. Paysandú: Lorenzo Geyres-Quebracho [26] (51–76), Queguayár [2] (77, 78). **Alto Madidi regiolect** [4]. BOLIVIA. Dpto. La Paz: Apolo-Madidi [4] (BH88–91).

‘caraguata’ [3] ARGENTINA. Entre Ríos: Las Piedras [1] (1), Ibicuy [1] (2), Gualaguaychú [1] (3).

S. cinnamomea [24] ARGENTINA. 1992–93: Corrientes: Mercedes [2] (AJ21, AJ22), Caza Pava [1] (MP24). Entre Ríos: Parque Nacional El Palmar [1] (MP23). 2003–07: Corrientes: Estancia El Socorro [9] (1–5, 7–10), Mercedes [1] (1), Colonia Pellegrini [2] (11,12). Entre Ríos: Gualaguaychú [1] (13). URUGUAY. 2003–07: dpto. Paysandú: Lorenzo Geyres [5] (14–18), San Javier/Río Negro [1] (RF19), Villa Soriano/Río Negro [1] (RF20).

APPENDIX 2: localities at which habitat use data were obtained

Localities are shown in Fig. 3. Numbers in [] indicate number of individuals per locality.

S. ruficollis [110] ARGENTINA. Corrientes: Colonia Pellegrini [5], Estancia El Socorro [3]. Entre Ríos: Gualaguaychú [14], Larroque-Urdinarraín [15], Arroyo Baru-San Salvador [27], Estancia La Marita [3]. Buenos Aires: Saladillo [12]. Santa Fé: Sauce Viejo [4]. URUGUAY. Dpto. Paysandú: Lorenzo Geyres-Quebracho [23], Queguayár [4].

‘caraguata’ [14] ARGENTINA. Entre Ríos: Gualaguaychú [10], Ibicuy [1], Las Piedras [1], Arroyo Ñancay [1], San Juan Poriahú [1].

APPENDIX 3: specimens examined

S. ruficollis. AMNH: 156535, 514650–653, 514656–662, 789493, 798446, 798486–492, 798494, 798495, 798497–507, 798510–519, 799118, 810666, 825230. FML: 2123, 2141, 2176, 8798, 9603, 9770, 9793–95, 9801–02. MAS: 4749. MNHN: 5781, 5782, 5784, 5785, 6111, 6113, 6114, 6116.

‘caraguata’. MLP: 14044. See Morphology for two additional live specimens.

S. cinnamomea. AMNH: 320211, 320653, 320654. MNHN: 6022, 6031, 6108, 6119, 6121. Museo Ornitológico de Berisso: no number assigned.



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