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Plumage variability and taxonomy of the Capped Seedeater *Sporophila bouvreuil* (Aves: Passeriformes: Emberizidae)

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Abstract

The species *Sporophila bouvreuil* comprises four subspecies: *S. b. bouvreuil*, *S. b. pileata*, *S. b. saturata* and *S. b. crypta*. The males of each subspecies differ in plumage whereas the females and juveniles are very similar and difficult to identify to subspecies. Here we use external morphological characters, mostly plumage, to examine the validity of the subspecies. A total of 209 specimens was examined (131 *S. b. bouvreuil*, 29 *S. b. crypta*, 43 *S. b. pileata* and 6 *S. b. saturata*). Although morphological measurements did not separate any taxa, plumage patterns support recognition of two taxonomic units, one of birds having reddish brown male plumage and the other of birds with grayish to white male plumage. Discrete diagnostic characters and sympatry in SE Brazil allow separation of *Sporophila pileata* (Sclater 1864) from *S. bouvreuil* (Müller 1776). On the other hand, *S. b. saturata* Hellmayr 1904 and *S. b. crypta* Sick 1968 should be considered synonyms of *S. bouvreuil*.

Key words: taxonomy, *Sporophila bouvreuil*, Capped Seedeater, Aves, Emberizidae

Resumo

O táxon *Sporophila bouvreuil* compreende quatro subespécies: *S. b. bouvreuil*, *S. b. pileata*, *S. b. saturata* e *S. b. crypta*. Os machos apresentam um padrão de plumagem distinto, enquanto as fêmeas e jovens possuem a plumagem semelhante, sendo difícil identificar com segurança a qual subespécie pertence. Este trabalho teve como objetivo determinar, por meio de caracteres morfológicos externos, a validade dos táxons deste complexo. Foram analisados 209 espécimes, sendo 131 *S. b. bouvreuil*, 29 *S. b. crypta*, 43 *S. b. pileata* e seis de *S. b. saturata*. As análises dos caracteres morfométricos não apontaram diferenças significativas entre os táxons, enquanto que os padrões de coloração de plumagem evidenciaram dois grupos distintos, um composto por aves com o dorso e ventre marrom-avermelhados e outro composto por aves com dorso e ventre cinza ou cinza-esbranquiçados. A presença de caracteres diagnósticos únicos para cada um destes grupos e a sua simpatria no sudeste do Brasil permite reconhecer *Sporophila pileata* (Sclater 1864) e *S. bouvreuil* (Müller 1776) como espécies plenas, enquanto que *S. b. saturata* Hellmayr 1904 e *S. b. crypta* Sick 1968 devem ser considerados como sinônimos de *S. bouvreuil.*

Palavras-chave: Taxonomia, *Sporophila bouvreuil*, caboclinhos, Aves, Emberizidae

Introduction

The genus *Sporophila* (Emberizidae) is among those with a very complex taxonomy. Intra- and interspecific variation is complex, geographic variation is confusing and has not been rigorously investigated, and descriptions of several species were based on only a single or a few individuals. Because of this, delimitation of evolutionary units in this genus is problematic, and the validity of some species, such as *S. melanops*, *S. zelichi* and *S. ardesiaca*, is controversial (Ouellet 1992).

The Capped Seedeater *Sporophila bouvreuil* is one of the best known species in a group of 11 very similar species widespread in South America (Sick 1997; Restall *et al.* 2007). The Capped Seedeater is currently composed of

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four subspecies: *S. b. bouvreuil* (Müller 1776), *S. b. pileata* (Sclater 1864), *S. b. saturata* Hellmayr 1904 and *S. b. crypta* Sick 1968. All subspecies are characterized by a black pileum and black wings and tail, while the rest of the body may vary in color. The nominate subspecies, originally described as *Loxia bouvreuil* Müller 1776, is based on "*Bouvreuil de l'isle de Bourbon*" (plate attributed to Daubenton and Daubenton 1765–66) and was included in the genus *Sporophila* by Cabanis (1851) in his *Sporophila aurantia*. The specific epithet, *bouvreuil*, returned 128 years later when Hellmayr (1904) restored the original name given by Müller. This name, because it was not latinized, had not yet been universally accepted (*e.g.* Wied 1830; Swainson 1837; Gray 1844). *Spermophila pileata* was described by Sclater (1864) based on a single specimen collected by Natterer in what is today Jaguariúna in the state of São Paulo. It was subordinated to *Sporophila bouvreuil* by Hellmayr (1938). *Sporophila saturata* was described by Hellmayr (1904) based on a single male specimen from the state of São Paulo. This author called attention to the similarity between it, *S. bouvreuil* and *S. pileata* ("*similes sed colore supra subtusque multo obscuriore*"). Given the similarity described by Hellmayr (1904, 1938), Pinto (1944) considered *S. saturata* to be subordinate to *S. bouvreuil*. Sick (1968) described *S. b. crypta* based on specimens from Lagoa Feia (Campos dos Goytacazes, Rio de Janeiro, Brazil), in which plumage in males was similar to that of females. However, it was noted in that description that these males may have been confused with subadults of the nominate form because of the presence of black feathers in the pileum and yellowish brown feathers on the upper and underside (Sick 1968). Whereas males of the *S. bouvreuil* complex, especially *S. b. bouvreuil* and *S. b. pileata*, are considered to be easily identifiable (Sharpe 1888; Hellmayr 1938; Meyer de Schauensee 1952; Sick 1967, 1968, 1997; Ridgely & Tudor 1989; Restall *et al.* 2007), females cannot be identified to species without knowing the location in which they were found, due to the lack of diagnostic characters (Meyer de Schauensee 1952; Ridgely & Tudor 1989; Sick 1997). Another complication arises from the moult that follows the reproductive period, when male plumage is very similar to that of females or immature males (Sick 1997).

Today, the four accepted taxa in this complex are found in open areas in Surinam and French Guiana, from the Amazon (Amapá, Pará) to the northeastern, eastern, central-western and southern areas of Brazil, in eastern Paraguay, and in northeastern Argentina (Misiones and Corrientes; Meyer de Schauensee 1952, 1966; Sick 1967, 1997; Ridgely & Tudor 1989; Stotz *et al.* 1996; Machado & Silveira 2010). The nominate form occurs from Amazonas to central and southern Brazil. *Sporophila b. pileata* is found in Brazil in the states of São Paulo, Minas Gerais and Mato Grosso, as well as in Paraguay and Argentina. *Sporophila b. saturata* occurs only in and near Ipiranga, a part of the city of São Paulo, and around the city of Mogi das Cruzes. Finally, *S. b. crypta* is endemic to the state of Rio de Janeiro (Meyer de Schauensee 1952; Sick 1967).

The taxonomic units that today are grouped within *S. bouvreuil* have never been the subject of a rigorous taxonomic revision. Here, we use external morphological characters to examine geographic variation in the *Sporophila bouvreuil* complex in an attempt to resolve the status and geographic distribution of its taxonomic units.

Material and methods

We examined a total of 209 museum specimens of *Sporophila bouvreuil*. These included specimens of *S. b. bouvreuil* (n = 131), *S. b. pileata* (43), *S. b. saturata* (6) and *S. b. crypta* (29), including the type series of the latter. We also examined the holotypes of *Spermophila pileata* Sclater (= *Sporophila b. pileata*), *Loxia brevirostris* Spix (= *S. b. bouvreuil*) and *Sporophila pileata paraguayensis* Chubb, as well as photographs of the iconotype of *Loxia bouvreuil* Müller (= *S. b. bouvreuil*) and the paratype of *Sporophila saturata* Hellmayr. A descriptive list of the material examined is found in Appendix I.

Morphometric characters (exposed culmen, bill width and depth, wing, tail and tarsometatarsus length) were all measured with calipers to 0.1 mm precision (following Baldwin *et al.* 1931). The left wing and tarsometatarsus were always measured. Samples sizes vary because measurements of some characters were not possible on some specimens. Morphometric characters were analyzed using ANOVAs, analyzing males and females separately. Scatterplots comparing morphometric variables among the taxa were also generated.

Plumage coloration was classified following Munsell (1994). Each specimen was analyzed without prior knowledge of its origin or taxonomic unit and later grouped according to its smallest diagnosable unit. Bill color of adult males, classified as black, brown, yellowish brown or yellow, was also used. An attempt to control for plumage phase was based on either an indication in the specimen itself or the date of its collection. Plumage phase was

used to define reproductive and moulting periods. Once specimens were classified using color patterns, we tested whether *S. b. crypta* might be confused with subadult *S. b. bouvreuil* due to black feathers in the pileum or brownish yellow feathers on the body, following suggestions by Sick (1967, 1968, 1997).

The locality of each specimen was plotted on maps using ArcView 3.3 (Environmental Systems Research Institute 2002). We used location information on the labels of museum specimens, and additional data from published records and field observations supplemented the above sources. Details of the distribution and seasonal movements are shown in Machado & Silveira (2010).

Results

Morphometrics. Morphometric characters did not discriminate any diagnosable unit (Fig. 1) and also did not match the variation found in plumage characters. When pairs of variables were analyzed or plotted together, the four taxonomic units were similar and all comparisons between taxonomic units were non-significant (ANOVA, $p > 0.05$, Table 1).

TABLE 1. Morphological measurements as mean, (SD) and [sample size], compared among taxonomic units of the *Sporophila bouvreuil* complex. No data are presented for females of *S. b. saturata* because females of this form are not known.

Character	Sex	*S. b. bouvreuil*	*S. b. pileata*	*S. b. saturata*	*S. b. crypta*
Culmen	♂	7.7 (0.5) [69]	7.7 (0.5) [17]	7.9 (0.3) [5]	7.6 (0.4) [18]
	♀	7.9 (0.5) [20]	7.5 (0.5) [5]		8.0 (0.4) [8]
Bill depth	♂	6.3 (0.4 [61]	6.4 (0.4) [17]	6.3 (0.4) [5]	6.3 (0.3) [16]
	♀	6.4 (0.5) [19]	6.4 (0.3) [4]		6.4 (0.4) [6]
Bill width	♂	5.0 (0.4) [62]	5.2 (0.5) [16]	5.2 (0.3) [5]	5.1 (0.2) [16]
	♀	5.1 (0.4) [19]	5.0 (0.0) [4]		5.4 (0.3) [7]
Wing length	♂	52.0 (1.8) [69]	51.6 (1.4) [19]	52.6 (2.0) [5]	51.7 (1.6) [19]
	♀	51.2 (2.0) [19]	48.6 (1.6) [5]		49.0 (1.4) [8]
Tail length	♂	42.4 (3.4) [65]	45.0 (2.5) [17]	43.2 (2.8) [5]	44.1 (3.5) [19]
	♀	41.8 (3.5) [20]	40.4 (3.9) [5]		44.1 (3.3) [8]
Tarsus length	♂	13.4 (1.0) [70]	13.1 (0.9) [19]	13.2 (1.6) [5]	13.6 (0.5) [19]
	♀	13.4 (0.9) [20]	12.7 (1.1) [5]		13.4 (0.8) [8]

Plumage patterns. Adult males: Wing, tail and pileum coloration was similar among all specimens and hence uninformative for taxonomic analysis. However, we were able to find two distinct, non-overlapping groups based on ventral and dorsal colors (Figs. 2–4).

A group of 35 specimens was formed by those in which ventral plumage varies from light gray (10YR7/2; in 57,90%) or pinkish gray (5YR7/2; 31,58%) to light yellowish brown (10YR6/4; 10,52%), combined with a dorsal plumage of dark grayish brown (10YR4/2; 94,74%) or light reddish brown (5YR6/3; 5,26%). Black feathers (dorsal or ventral) were found in a few specimens (*e. g.* MHNT 3039 and MZUSP 23753). These specimens form a consistent group of "grayish-white" birds with patterns consistent within geographic regions; no indications of intergradation or clinal variation were found. Specimens in this group were in agreement with descriptions found in the literature (Sclater 1864, 1871; Sharpe 1888; Hellmayr 1904, 1929; Chubb 1910; Sick 1967, 1997) and refer to *Sporophila b. pileata* (including *S. pileata paraguayensis*, long considered a synonym of the latter).

The ventral regions of the second group, comprising 119 specimens, were either pale brown (10YR6/3; 56,84% of the samples), reddish brown (5YR5/4; 42,10%) or dark yellowish brown (10YR4/4; 1,05%). More than one plumage color (10YR6/3 and 5YR5/4) occurred in 34 of these individuals, which were found in a variety of locations in the Brazilian states of Pará, Pernambuco, Bahia, Espírito Santo, Rio de Janeiro and São Paulo. This suggests that color may change with age. The dorsal region varied from reddish brown (5YR4/4; 38,94%) and dark

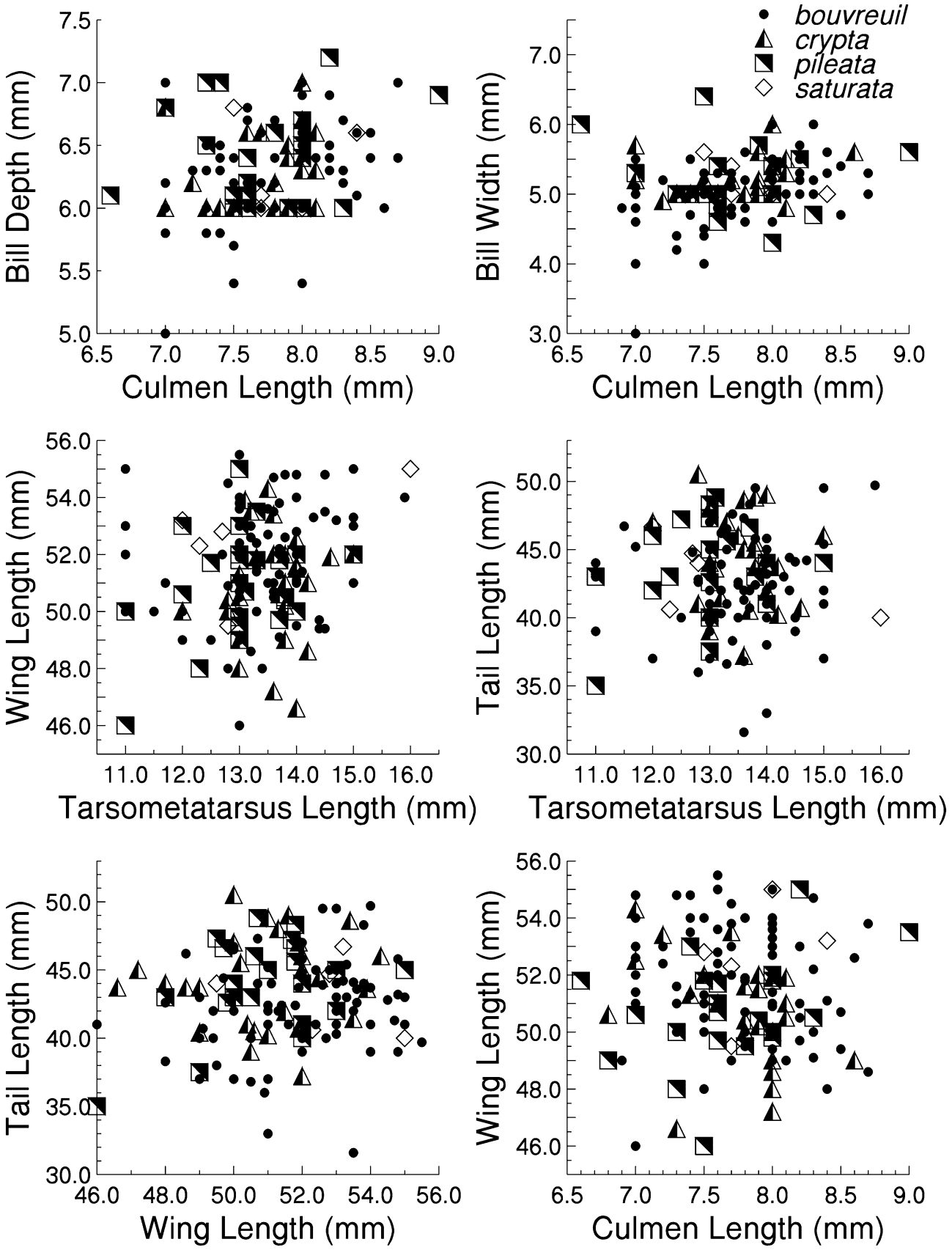

FIGURE 1. Scatterplots of morphological variables. Note that all taxonomic units have similar variation in morphology and that none forms a distinct grouping of points.

FIGURE 2. Ventral view of adult males of the *Sporophila bouvreuil* complex (specimen series from the MZUSP).

grayish brown (10YR4/2; 46,31%) to yellowish brown (10YR5/4; 14,75%). This "reddish" group of birds presents a color pattern described for *S. bouvreuil* (Vieillot 1823; Spix 1825; Lesson 1831; Sharpe 1888; Hellmayr 1904; Sclater 1871; Ridgely & Tudor 1989; Sick 1997), although they have been referred to as red-brown (Sick 1967), light-red (Snethlage 1914) and yellowish (Buffon & Montbeillard 1778). Specimens within this group include those individuals named as *S. b. bouvreuil*, *S. b. saturata* and *S. b. crypta*.

In the *S. b. saturata* specimens, the ventral region varied among reddish brown (5YR5/4), pale brown (10YR6/3), and dark yellowish brown (10YR4/4), while dorsal color was generally reddish brown (5YR4/4). Dorsal coloration of all specimens of *S. b. saturata* was similar to that of 32 specimens of the nominate form (5YR4/4) from the states of Pará, Tocantins, Maranhão, Pernambuco, Alagoas, Bahia, Espírito Santo and Minas Gerais. The ventral colors of the *S. b. saturata* individuals (10YR6/3 and 5YR5/4) were also found in 80 specimens attributed to *S. b. bouvreuil*, from the states of Pará, Maranhão, Tocantins, Pernambuco, Alagoas, Bahia, Mato Grosso, Goiás, Distrito Federal, Espírito Santo, Rio de Janeiro and Minas Gerais. Color patterns of *S. b. saturata* did not concur with descriptions in the literature that state that this taxon is "chestnut rather than cinnamon" (Ridgely & Tudor 1989) or "chestnut-brown" (Ihering 1898). Sometimes, the color has been described as merely darker than the nominate form (Hellmayr 1938) or as "*colore supra subtusque multo obscuriore, saturate cinnamomeo-brunneo*" (Hellmayr 1904).

The color pattern attributed to *S. b. crypta* was found in several males of the nominate form. Specimens considered to be *S. b. crypta* were pale brown (10YR6/3) ventrally and yellowish brown (10YR5/4) or dark grayish brown (10YR4/2) dorsally. *S. b. bouvreuil* specimens from other locations also had these colors (Pará MNRJ 17774, Bahia MZUSP 14340, Goiás MZUSP 15316, Minas Gerais DZUFMG 3965, Surinam RMNH 38278, also a breeding male). Therefore, no color characters uniquely identify *S. b. crypta*.

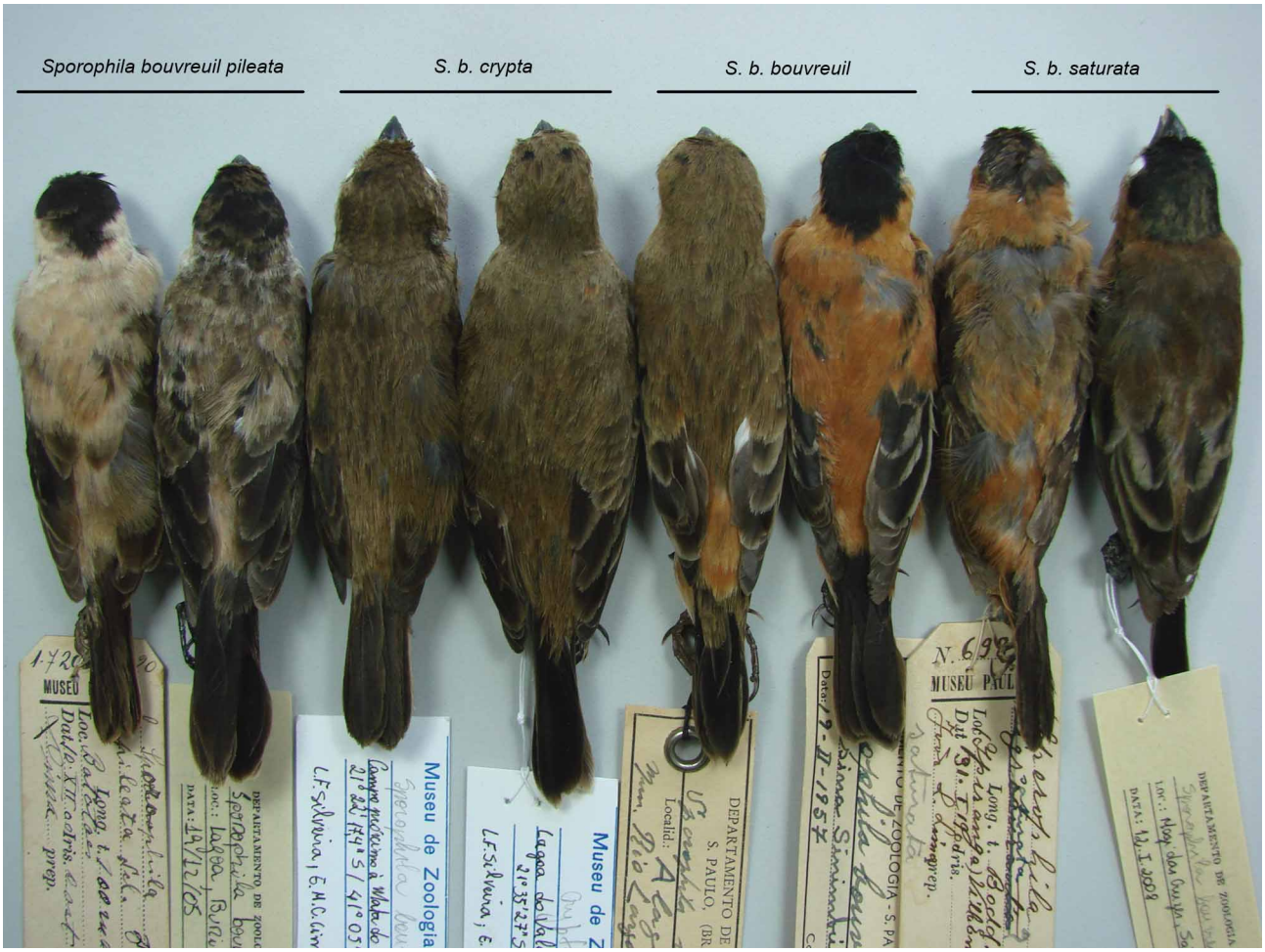

FIGURE 3. Dorsal view of adult males of the *Sporophila bouvreuil* complex (specimen series from the MZUSP).

Adult female. Female coloration showed no discernible geographic variation. Therefore, it was impossible to use female color pattern as a diagnosis for the *Sporophila bouvreuil* complex. The standard female plumage is brown (10YR4/3, 10YR5/3, 10YR7/3, 10YR7/4, 10YR8/4), sometimes tending towards yellowish (10YR3/4, 10YR4/4, 10YR5/4, 10YR5/6, 10YR6/4) or grayish (10YR3/2, 10YR4/2), with a lighter ventrum than dorsum.

Distribution. "Reddish" birds, attributed to *S. b. bouvreuil*, *S. b. saturata* and *S. b. crypta* are found in open areas throughout most of northern South America, from Suriname (specimens in RMNH) and French Guiana (specimens in ANSP) to Argentina and throughout Brazil in open habitats (Fig. 5; Machado & Silveira 2010). *Sporophila pileata* is limited to the southeast of Brazil (in the states of Minas Gerais, São Paulo, Mato Grosso do Sul, Goiás, Paraná, Rio Grande do Sul) and adjacent countries (Paraguay and Argentina). This species is found in the *cerrado* and open areas within the Atlantic Forest formation and its transition zone with the *cerrado*, in the Pantanal of Mato Grosso, in the southern grasslands of Rio Grande do Sul, and in the Chaco of Paraguay and Argentina. *Sporophila bouvreuil* and *S. pileata* are found in sympatry in Minas Gerais and São Paulo states (Fig. 5; Machado & Silveira 2010).

Discussion

While morphometrics do not separate any of the taxonomic units in the *S. b. bouvreuil* complex, color patterns suggest that two taxa can be recognized, *S. b. bouvreuil* and *S. b. pileata*. Our examination of the relevant specimens found no support for the assertion that intermediates exist between those two subspecies (Hellmayr 1938, based on specimens collected by Natterer in 1819), in agreement with Sclater (1871).

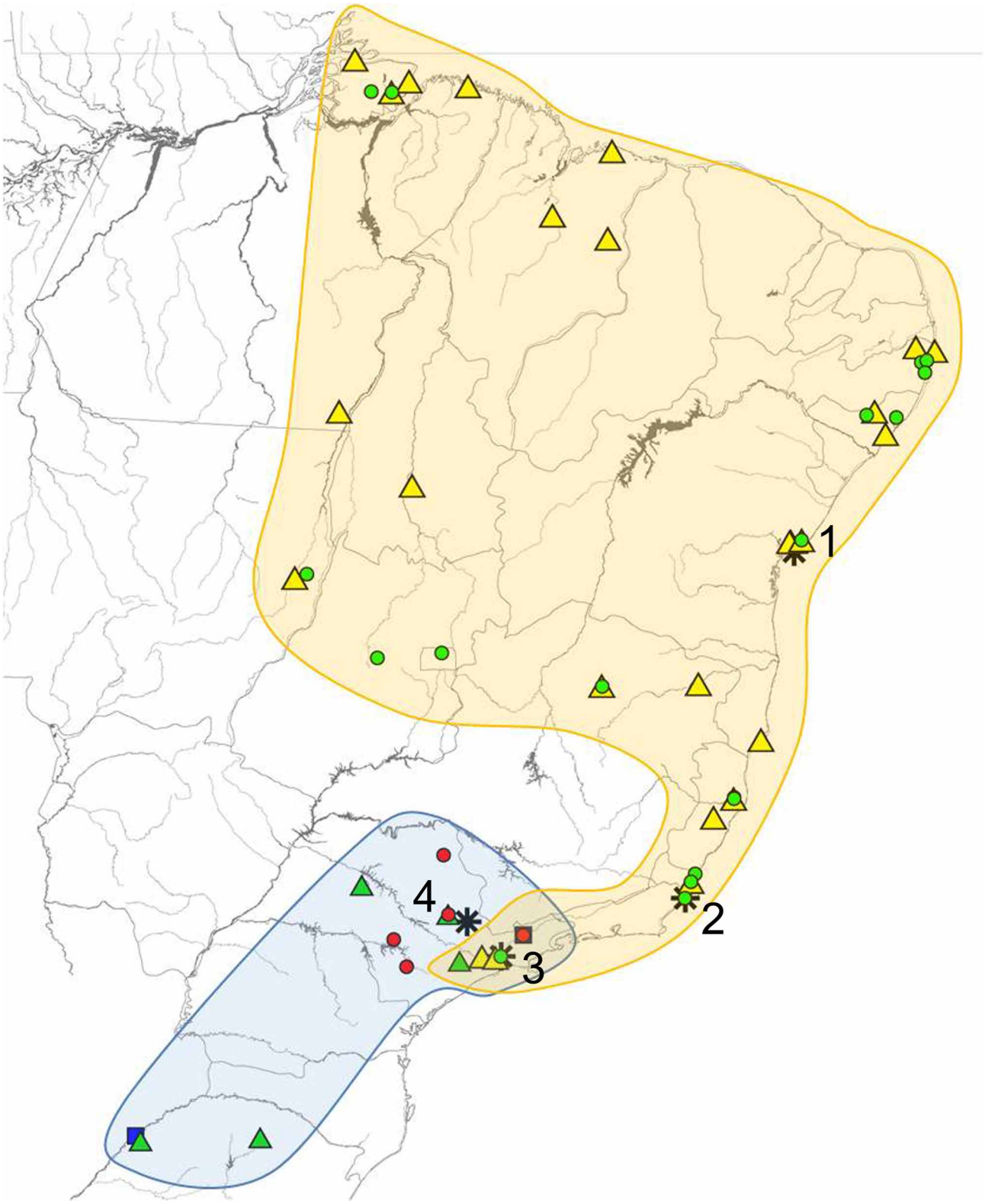

FIGURE 4. Map illustrating the geographic distribution of the ventral color patterns of adult male birds in the *S. bouvreuil* complex. Reddish brown ventral coloration is indicated by yellow triangles, light yellowish brown by blue squares, light gray by green triangles, pale brown by green circles, pinkish gray by red circles. The type localities are indicated by the asterisks: 1: *S. b. bouvreuil*; 2: *S. b. crypta*; 3: *S. b. saturata*; 4: *S. b. pileata*. Note two character groupings: one formed by *S. b. pileata* in blue, and the other by *S. b. bouvreuil*, *S. b. saturata* and *S. b. crypta* in orange, showing an area of sympatry in the state of São Paulo.

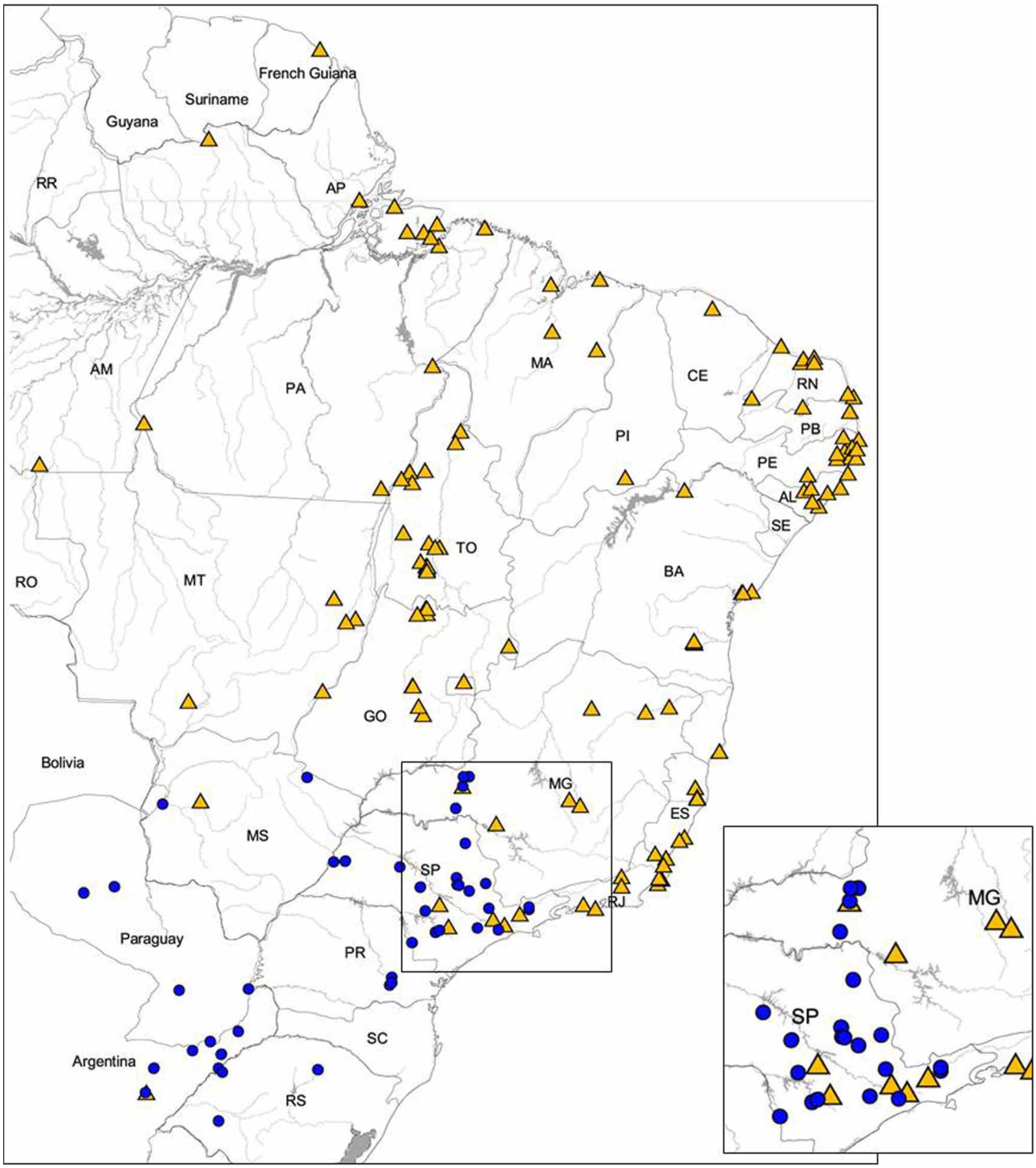

FIGURE 5. Geographic distribution of *Sporophila bouvreuil* (yellow triangles) and *Sporophila pileata* (blue circles) based on specimens, literature and field work. Inset: area of sympatry in the states of Minas Gerais (MG) and São Paulo (SP).

Color patterns that purportedly separate *S. b. bouvreuil* from *S. b. saturata* appear to reflect individual or age-related variation. Indeed, the diagnosis of *S. b. saturata* is particularly weak, leading to the attribution of individual specimens to either nominate *bouvreuil* or to *saturata*, depending on the author. For example, Pelzeln (1868) treated the "Goyao" specimens collected by Natterer as *Spermophila aurantia* (= *S. b. bouvreuil*), but Hellmayr (1904) used one of these specimens as a second example ("ein zweites Exemplar") in his description of *S. b. saturata*. Likewise, specimens (MZUSP 698; 3098) identified (Ihering 1898) and confirmed (Ihering 1907) as *Spermophila nigroaurantia* (= *S. b. bouvreuil*) were later considered to be *S. b. saturata* (Pinto 1944). Sick

(1967, 1997) did not refer to *S. b. saturata* as a valid taxon, nor did he state why he did not. Krabbe (2007) commented that Lund, in 1833, collected three specimens of *S. b. saturata* in the city of Mogi das Cruzes. Krabbe (2007) also proposed that *S. b. saturata* develops a distinctive non-reproductive plumage, thereby suggesting that the subspecies is valid. However, we find no evidence to support this claim and we suggest that color variation within the species is the reason for the confusion in naming of the taxa.

Similarly, the color description of *S. b. crypta* is imprecise; it has been described as simply light brown (Sick 1967, 1968, 1997). Some male songbirds have thought to be capable of reproduction without acquiring reproductive plumage (Amadon 1966). That this might apply to *S. b. pileata* was noted by Belton (1994) who, in 1973, collected a male "in female plumage" together with a male in adult male plumage, both with well-developed, reproductive testes. Paedomorphosis is particularly frequent in *Sporophila* and was reviewed by Areta (2009). Sick (1997) also affirmed that males of the genera *Sporophila* and *Sicalis* may reproduce without having adult plumage. Males in subadult plumage collected at the Campos dos Goytacazes in October 2007 also had developed testes (10x10 mm), indicating reproductive activity. Five other individuals in breeding condition collected there (MZUSP 78842, 78843, 78850, 78851, 78852) had typical *S. b. bouvreuil* color patterns. Thus, again, confusion associated with natural color variation may be the cause of the recognition of the subspecies *S. b. crypta*.

Females offer no support for the separation of any of the subspecies. For example, dorsal plumage of female *S. b. bouvreuil* is described as olive-brown or brown (Sclater 1871; Sharpe 1888; Snethlage 1914; Ridgely & Tudor 1989; Sick 1997). The ventral coloration is described as light brown, ochraceous or yellowish white (Sharpe 1888; Snethlage 1914; Ridgely & Tudor 1989). Ventral coloration in female *S. b. pileata* is also described as brown, yellowish brown or yellowish white (Chubb 1910; Ridgely & Tudor 1989; Sick 1997), while the dorsal color is also brown or olive brown (Sclater 1871; Ridgely & Tudor 1989; Sick 1997). Forty years after the description of *S. b. crypta*, females have still not been described.

Plumage color variation. Age-related variation in plumage color occurs in many species of *Sporophila*, including *S. minuta* (Fig. 6), *S. insularis*, *S. schistacea* and *S. frontalis* (Sick 1997; Restall 2006; Restall *et. al.* 2007; Machado *pers. obs.*), as well as *S. falcirostris*, *S. collaris*, *S. nigricollis*, *S. intermedia* and *S. plumbea* (Sick 1997; Restall 2006). For example, three shades of plumage can be seen in one location in *Sporophila minuta* (Fazenda Santa Cecília, Roraima, Brazil; series in MZUSP), where color variation includes yellowish red (5YR4/6; MZUSP 73439), strong brown (7.5YR5/6; MZUSP 73446) and light brown (7.5YR6/4), along with strong brown and reddish yellow (7.5YR6/6; MZUSP 73447). This variation is probably associated with age, with older individuals being darker. Similarly, this kind of age variation may have influenced the description of some subspecies, such as *S. b. saturata* (Fig. 6). More refined studies are required to describe the ontogenetic development of this variation.

Field data from two captures of a male of "*S. b. saturata*" near Mogi das Cruzes support the hypothesis that variation in ventral coloration is age-related. At first capture (15 November 2006) this male retained vestiges of brown on the pileum and was mostly non-uniformly reddish brown on the rest of the body (Fig. 7A). Less than two years later (12 January 2008) when the male was again encountered, the pileum was totally black while the remainder of the body was uniformly reddish-brown, without vestiges of brown (Fig. 7B). Despite our very reduced sample, these are the first data that provide a temporal frame for age-related plumage changes.

Eclipse plumage. Eclipse plumage occurs during the non-reproductive season in some species of birds and in *S. pileata* occurs only in males (Sharpe 1888; Hellmayr 1938; Sick 1997). Blaauw (1919) described the transition in which a light brown individual acquires a dark pileum and its bill color changes from yellow to black during the winter; then the pileum changes returns to a uniform light brown and the bill color changes from black to yellow, this cycle of change occurring once per year. Eclipse plumage in *S. pileata* has been noted in captive individuals, with less of a change in color in older males (Alvarenga *pers. com.*). Only Sharpe (1888) suggested that *S. bouvreuil* also goes through eclipse plumage.

Sympatry. Machado & Silveira (2010) found *S. pileata* and *S. bouvreuil* sympatric in the western Minas Gerais State, near Indianópolis (Fig. 5). These species have also been found in close proximity in southwestern and central São Paulo State during the breeding and non-breeding season (records obtained from the literature, field and museum specimens). Both species may be also found near Itirapina (São Paulo; field data). In southwestern São Paulo, records are relatively close to one another near Botucatu (*S. bouvreuil*—Guzzi & Donatelli 2003) and Avaré (*S. pileata*—MZUSP 54127, the two separated by 52 km) and Itapetininga (*S. bouvreuil*—Figueiredo *et al.* 2000)

and Aracaçú (*S. pileata*—MCZ 265011, separated by 32 km). In the southeast, *S. bouvreuil* and *S. pileata* were recorded within 40 km of each other near Franco da Rocha (field data) and Itatiba (*S. pileata*—MZUSP 10686), São José dos Campos (*S. bouvreuil*—Pelzeln 1868) and Tremembé (*S. pileata*—MHNT 3039, 3140) and São José dos Campos (*S. bouvreuil*—Pelzeln 1868) and Taubaté (*S. pileata*—MHNT 3141), respectively. The two species are found closer together near São Paulo (*S. bouvreuil*—MZUSP 698) and São Bernardo do Campo (*S. pileata*—RG 7556; 18 km), and Mogi das Cruzes (*S. bouvreuil*—MZUSP 77828, 77829, 77830, 79445, NMW 20334) and São Bernardo do Campo (*S. pileata* —RG 7556; 33 km, respectively, Fig. 5). Both species have been recorded in the state of Mato Grosso do Sul, yet not in sympatry. For a species that regularly migrates greater distances (Silva 1999), these must be considered short distances. In fact, the distributional pattern suggests a broad contact zone between the two species (Machado & Silveira 2010; Silva 1995, 1999). More field work must be conducted to determine more precisely the extension of this contact zone.

FIGURE 6. Ventral view of adult male *Sporophila bouvreuil* in the Moji das Cruzes and São Paulo regions (attributed to *S. b. saturata*) and *S. m. minuta*, showing color variation that is most likely due to age rather than phylogeny (specimen series from the MZUSP).

Taxonomic implications. The lack of intermediate forms between *S. b. pileata* and the remainder of the *S. bouvreuil* complex, the sympatry between these two taxa, and the unambiguous diagnostic characters permit recognition of *S. pileata* (Sclater 1864) as a distinct species under both the biological species concept and the phylogenetic species concept. Males of *S. pileata* are recognized by the light gray (10YR7/2), pinkish gray (5YR7/2) or light yellowish brown (10YR6/4) ventral color, and are found in the states of Rio Grande do Sul, Paraná, São Paulo, Minas Gerais and Mato Grosso do Sul, as well as adjacent Argentina and Paraguay (Fig. 5; Machado & Silveira 2010). It is interesting to note that Campagna *et al.* (2009), in a molecular study including the 11 known species of small *Sporophila* ("capuchinos"), found the highest intraspecific divergence between *S. b. pileata* and *S. b. bouvreuil*.

The remaining taxa of the *S. b. bouvreuil* complex do not warrant continued recognition, because individuals classified as *S. b. crypta* and *S. b. saturata* form part of the natural variation found in the nominate form, which occurs in the same area as *S. b. crypta*. As a distinct species, *S. bouvreuil* may be diagnosed by its pale brown (10YR6/3) ventral color, which may vary to dark yellowish (10YR4/4) or reddish (5YR5/4) brown. This taxon occurs in Surinam, in French Guiana, from northern and northeastern to central-western and southeastern Brazil, and in northeastern Argentina (Fig. 5; Machado & Silveira 2010).

FIGURE 7. A: A male captured and color-banded near Moji das Cruzes, São Paulo, on 16 November 2006, and B: the same individual on 12 January 2008. Note the color change.

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APPENDIX I. List of the specimens examined.

Sporophila bouvreuil bouvreuil—131: **BRAZIL: Pará**: (1 ♂—BMNH 1845.8.25.76); (1 ♂—ZSM 1478, type of *Loxia brevirostris* Spix); Quatipuru (2 ♂—MPEG 12636, MNRJ 17773); Santana do Araguaia (1 ♂—MPEG 49193); Ilha da Roça (associada à Ilha de Marajó) (1 ♂—MNRJ 17774); Ilha de Marajó, Rio Arari (1 undetermined—MPEG 548); Ilha de Marajó, Soure (1 ♂—MPEG 34395); Ilha de Marajó, Chaves (1 ♂—MPEG 50519); Ilha de Marajó, Cachoeira do Arari (4 ♂—MPEG 50519, MPEG 22515, MNRJ 44083, MNRJ 44085; 2 ♂ juvenile—MPEG 22518, MNRJ 44087; 2 ♀—MNRJ 44084, MNRJ 44086; 2 undetermined—MNRJ 44088, MNRJ 44089). **Tocantins**: Santa Rosa do Tocantins (1 ♂—MZUSP 76112). **Maranhão**: Bacabal (1 ♂—MPEG 49801); Caxias (2 ♂—MPEG 50853, MPEG 50855; 2 undetermined—MPEG 50854, MPEG 50856); Santo Amaro (1 ♂—MZUSP 6816); São Bento (1 ♂—MNRJ 14741). **Ceará**: Itapipoca (1 ♂ juvenile—MZUSP 42122; 1 ♀—MZUSP 42123). **Paraíba**: Mamanguape (1 ♂ juvenile—MZUSP 40600). **Pernambuco**: (3 ♂—BMNH 1885.12.14.396, BMNH 1885.12.14.397, BMNH 1885.2.10.117), Exu (1 ♂—MNHN 1998.1146); Itamaracá (2 ♂—MZUSP 18610, MZUSP 18612; 1 ♀—MZUSP 18609); São Bento (1 ♂—MZUSP 18611); Vicência (1 ♂—MZUSP 63487); São Lourenço da Mata (1 ♂—MNRJ 24774); Mercês (1 ♂—MNRJ 24918); Vitória de Santo Antão (1 undetermined—MZUSP 34286). **Alagoas**: Rio Largo (1 ♂—MZUSP 37750, MZUSP 37751); Palmeira dos Índios (1 ♂—MZUSP 37751); Sinimbú (5 ♂—MZUSP 37751, MZUSP 39329, MZUSP 39330, MZUSP 39331, MZUSP 39332); Quebrângulo (1 ♂—MZUSP 39333). **Bahia:** (8 ♂—MNHN 1999.2211, MNHN 1999.2213, MNHN 1999.2212, MNHN 1858.878, BMNH 1885.12.14.394, BMNH 1885.2.10.115, BMNH 1885.12.14.393, BMNH 1885.12.14.395); Nova Viçosa (2 ♂—MHNT 4157, MHNT 4158); Ilha Bimbarra (1 ♂—MZUSP 14340); Camaçari (2 ♂—RG 9966, RG 9985); Curupeba (1 ♂—MZUSP 11340; 1 ♀—MZUSP 14342). **Goiás**: Aragarças (1 undetermined—MNRJ 31197); Jaraguá (2 ♂—MZUSP 15314, MZUSP 15316). **Distrito Federal**: Planaltina (1 ♂—MNRJ 14834). **Mato Grosso**: Pontal da Serra Azul (1 ♂—MZUSP 17531; 1 ♂ juvenile—MZUSP 17530); Molha Saco (1 ♂—MZUSP 35334); Serra do Roncador (1 undetermined—MZUSP 69400). **Espírito Santo**: Linhares (19 ♂—MBML 6355, MBML 6356, MBML 6358, MBML 6359, MBML 6361, MBML 6364, MBML 6365, MBML 6366, MBML 6369, MBML 6370, MBML 6371, MBML 6373, MBML 6374, MNRJ 26457, MNRJ 27083, MNRJ 27108, MNRJ 27109, MNRJ 27721, MNRJ 27724; 9 ♀—MBML 6357, MBML 6362, MBML 6363, MBML 6367, MBML 6368, MBML 6372, MBML 6375, MBML 6376, MBML 6377); Guarapari (2 ♀—MZUSP 28139, MZUSP 28140); Santa Teresa (1 ♂—MBML 6360); Cupido (1 undetermined—MNRJ 27110). **Rio de Janeiro**: (3 ♂—BMNH 1895.4.1.271, BMNH 1895.4.1.272, BMNH 1885.2.10.113); Campos dos Goytacazes (9 ♂—MZUSP 78842, MZUSP 78843, MZUSP 78844, MZUSP 78845, MZUSP 78846, MZUSP 78850, MZUSP 78851, MZUSP 78852, MZUSP 78853; 1 ♀—MZUSP 78849; 1 ♂ juvenile—MZUSP 78847); Itaguaí (1 ♀—MNRJ 31060, 1 undetermined—MNRJ 31061). **Minas Gerais**: Francisco Sá (2 ♂—DZUFMG 3963, DZUFMG 3965; 2 ♀—DZUFMG 3962, DZUFMG 3964); Jequitinhonha (1 ♂—MNRJ 31459). São Paulo: (1 ♂—MNHN 1892.1222). **SURINAM:** Sipaliwini (6 ♂—RMNH 72202, RMNH 38278, RMNH 72759, RMNH 72201, RMNH 39225, RMNH 38264).

Sporophila bouvreuil pileata—43: **BRAZIL: Mato Grosso**: Porto Espiridião (1 ♀—MNRJ 9595). **Mato Grosso do Sul** (1 ♀—MZUSP 13326). **Minas Gerais**: Água Suja (1 ♂—ZSM 11.1445) **São Paulo**: (1 ♂—MNHN 1892.221); Avaré (1 ♂—MZUSP 54127); Batatais (1 ♂—MZUSP 1720); Buri (2 ♂—MZUSP 76717, MZUSP 76718); Borda do Mato (1 ♂—BMNH 1885.2.10.118, type of *Spermophila pileata* Sclater); Ibiúna (1 ♂—MZUSP 23753; 1 undetermined—MZUSP 23754); Itararé (1 ♂—BMNH 85.2.10.118); Itatiba (1 ♂ juvenile—MZUSP 10686); Lins (5 ♂—MZUSP 26292, MZUSP 26293, MZUSP 26294, MZUSP 26296, MZUSP 26297; 1 ♀—MZUSP 262295); Santa Gertrudes (4 ♂—MZUSP 77831, MZUSP 77832, MZUSP 77833, MZUSP 77834); São Bernardo do Campo (1 ♂—RG 7556); Tremembé (1 ♂—MHNT 3039; 2 ♀—MHNT 3040, MHNT 3041). **Rio Grande do Sul**: Alegrete (1 undetermined—MCN 1434); Passo Fundo (1 ♂—MCN 2114); São Borja (2 ♂—MCN 1435, MCN 1436). **ARGENTINA:** Posada Misiones (1 ♂—MNHN: 1952.346). **PARAGUAY:** Sapucay (2 ♂—BMNH 1905.10.12.879, BMNH 1905.10.12.844, type of *Sporophila pileata paraguayensis* Chubb); Encarnacíon (1 ♂—ZSM 38.99); San Luís de la Sierra (6 ♂—ZSM 32.145, ZSM 32.146, ZSM 32.146, ZSM 32.147, ZSM 32.148, ZSM 32.149, ZSM 32.150, ZSM 32.151, ZSM 32.152).

Sporophila bouvreuil saturata—6: **São Paulo**: São Paulo (1 ♂—MZUSP 698; 1 undetermined—MZUSP 3098); Mogi das Cruzes (4 ♂—MZUSP 77828, MZUSP 77829, MZUSP 77830, MZUSP 79445).

Sporophila bouvreuil crypta—29: **Rio de Janeiro**: Campos dos Goytacazes, Lagoa do Valão (1 ♂—MZUSP 78848); Campos dos Goytacazes, Mata do Carvão (1 ♂—MZUSP 78854); Campos dos Goytacazes, Lagoa Feia (17 ♂—MNRJ 28887, MNRJ 30090, MNRJ 30091, MNRJ 30094, MNRJ 30096, MNRJ 30097, MNRJ 30099, MNRJ 32495, MNRJ 32496, MNRJ 32497, MNRJ 32498, MNRJ 32499, MNRJ 32500, MNRJ 32501, MNRJ 32502, MNRJ 32503, MNRJ 32504; 1 ♂ juvenile—MNRJ 30095; 8 ♀—MZUSP 78856, MNRJ 30093, MNRJ 32505, MNRJ 32506, MNRJ 32507, MNRJ 32508, MNRJ 32509, MNRJ 32510; 1 undetermined—MNRJ 32511, type series).