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Morphological variation in the Cinnamon Tanager *Schistochlamys ruficapillus* (Aves: Thraupidae)

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Abstract

The Cinnamon Tanager *Schistochlamys ruficapillus* inhabits semi-open grassy country, primarily in Brazil south of Amazonia. Three subspecies are currently recognized, one of which, *S. r. sicki*, is poorly known and endemic to the central Brazilian savannas (Cerrado). This paper analyses individual and geographic variation in this species on the basis of body measurements and plumage coloration. Larger birds are usually found farther south and at higher elevations, while smaller birds are found farther north and at lower elevations, as predicted by Bergmann's rule. Nevertheless, some unexpectedly small individuals (referable to *S. r. sicki*) can be found in central Brazil. Individual and geographical variation in plumage coloration is substantial, but it is not closely tied to variation in body size. Therefore, given the large number of specimens intermediate between the three subspecies, we propose to consider the Cinnamon Tanager a monotypic but highly variable species. The recognition of three subspecies by previous taxonomists was due to small sample sizes associated with large gaps in sampling.

Key words: birds, Cerrado, Neotropics, tanagers, taxonomy

Introduction

The Cinnamon Tanager *Schistochlamys ruficapillus* (Vieillot, 1817) inhabits semi-open grassy country with scattered bushes and low trees, and is especially common in high mountain meadows above treeline (Isler & Isler 1987; Sick 1997; Ridgely & Tudor 2009; Hilty 2011). It occurs from northeastern to central and southern Brazil, with recent records from Argentina and Paraguay (Chebez 1996; Sick 1997; Zapata 2003; Ridgely & Tudor 2009). Three subspecies are traditionally recognized (Storer 1970; Isler & Isler 1987; Dickinson 2003; Clements 2007; Hilty 2011). The nominotypical subspecies has been recorded from southern Goiás, south-central Minas Gerais, Espírito Santo, Rio de Janeiro, São Paulo, and Paraná in Brazil (Pinto 1944; Storer 1970), to southeastern Paraguay (Zapata 2003; Guyra Paraguay 2005) and northeastern Argentina (Chebez 1996). *Schistochlamys ruficapillus capistratus* (Wied-Neuwied, 1821) occurs from the extreme northern Minas Gerais northward, with records in Bahia, Alagoas, Pernambuco, Piauí, and Maranhão (Pinto 1944, 1954; Storer 1970). *Schistochlamys ruficapillus sicki* Pinto & Camargo, 1952, is the least-known subspecies, with published records from Serra do Cachimbo in southern Pará and Rio das Mortes in eastern Mato Grosso (Pinto & Camargo 1952, 1957; Storer 1970). Hilty (2011) referred birds from southern Pará to *S. r. capistratus*, contra Pinto & Camargo (1957), who referred specimens from there to *S. r. sicki*.

Although the Cinnamon Tanager occupies a large range and is fairly common where suitable habitat is available, being listed as a species of Least Concern (BirdLife International 2014), *S. r. sicki* is poorly known and very rare in collections (Pinto & Camargo 1952, 1957; Storer 1970). This subspecies is endemic to the Cerrado (Sick 1965), the largest savanna region in South America (Silva & Bates 2002) and considered a hotspot of biodiversity (Myers *et al.* 2000). The Cerrado is one of the regions of the world suffering major anthropogenic degradation (Ratter *et al.* 1997; Silva & Bates 2002); only 2.2% of its area is under legal protection (Klink & Machado 2005).

A poorly known and rare taxon like *S. r. sicki*, endemic to a highly threatened region, might at a first glance be worthy of conservation concern. However, it is well known that the subspecies concept has historically been misused and that many of the subspecies traditionally recognized do not survive meticulous revision (Patten & Unitt 2002; Zink 2004; Remsen 2010), especially if extensive samples are available (e.g. Lopes & Gonzaga 2012, 2014). Therefore, the taxonomic status of the three subspecies of *S. ruficapillus* deserves review, especially given that they differ minimally (Hilty 2011), showing a pattern of morphological variation that suggests the current classification represents a taxonomic artifact, possibly a cline.

Pinto & Camargo (1952) observed that variation in body size of *S. ruficapillus* “proceeds in a gradual way, like a true cline” [translated from Portuguese]. The intensity of plumage coloration also has been suggested to be clinal, because “the color of throat and breast shows its maximum intensity in the state of São Paulo (near its capital), becoming progressively faded [northward], reaching in Bahia the typical appearance of the race *S. r. capistratus*, which is characterized mainly by the extremely pale coloration of those parts” [translated from Portuguese] (Pinto & Camargo 1952). Nevertheless, Hellmayr (1929) observed that birds from Piauí, when compared with specimens from Bahia, “have the pileum generally rather more brownish and the anterior under parts slightly darker, while the dimensions are on average smaller”.

These observations strongly suggest that the currently recognized subspecies of *S. ruficapillus* might represent only taxonomic artifacts due to poor sampling, and that individual and geographical patterns of morphological variation in the species might be more complex than presently recognized. Given that, in this study we conducted a taxonomic revision of *S. ruficapillus* based on an extensive analysis of external morphological characters. We also comment on its habitat and on records that represent noteworthy range extensions for the species.

Taxonomic and nomenclatural history. *Schistochlamys* Reichenbach, 1850, was based on an illustration on plate 77 of the book “Avium Systema Naturale”. Reichenbach (1850) did not designate a type species for the genus. Sclater (1886) designated as the type *Tanagra capistrata* Wied-Neuwied, 1821, a name currently applied to a subspecies of *S. ruficapillus* (Dickinson 2003; Clements 2007). Correct usage of the name *Schistochlamys* has been debated elsewhere (Gregory 2000; ICZN 2002).

Saltator ruficapillus Vieillot, 1817, was based on a specimen from an unspecified South American locality. Hellmayr (1920) noted that the specimen label bears the inscription “Brésil, 1808”, and thereafter designated the type locality as Rio de Janeiro. Vieillot (1817) described this species as presenting “le front, le lorum, le ventre, d'un noir un peu teinté de roussâtre” [the forehead, lores and belly black, slightly washed reddish], apparently using the word “ventre” instead of “menton” [chin], and so incorrectly indicating that the belly of this species was black (Hellmayr 1906, 1920). Vieillot (1822) apparently tried to correct his previous mistake by stating that the species shows “la tête, la nuque et toutes les parties inférieures rousses” [the head, the nape and all the underparts reddish-yellow], which is also incorrect, because the Cinnamon Tanager has a reddish-yellow (or “cinnamon”) throat and breast, but a whitish belly. Vieillot (1822) continued to make problems when he repeated that “le front, les lorums et le ventre d'un noir un peu teinté de roussâtre”. Such errors resulted in the recognition of *Tanagra leucophaea* Lichtenstein, 1823, based on a specimen collected in “Brazil” and deposited in the Museum für Naturkunde (Lichtenstein 1823), as the valid scientific name for the Cinnamon Tanager for almost a century. The name proposed by Vieillot was adopted for this species only after examination of the holotype by Hellmayr (1920), even though a similar conclusion was presented decades before by Pucheran (1855).

The name *Tanagra capistrata* Spix, 1825, is treated as a junior synonym of *Saltator ruficapillus* Vieillot, 1817, by some authors (e.g. Hellmayr 1936). Nevertheless, the attribution of the authorship of *T. capistrata* to Spix is incorrect, because he explicitly stated that this name was a “Principe de Neuwied designata” (Spix 1825), therefore referring to the taxon described by Wied-Neuwied (1821), which is currently considered a subspecies of *S. ruficapillus* (see below). It is important to highlight that the illustration of the Cinnamon Tanager presented in Spix (1825) is quite inaccurate, the bird depicted being too dark, with the cinnamon color of the breast extending down to the belly, as Wied-Neuwied (1830) acknowledged.

Tanagra capistrata Wied-Neuwied, 1821, was described from an unspecified number of specimens collected in “Fazenda von Ilha, Campos Gerães”, southern Bahia, Brazil (Wied-Neuwied 1821). This brief description was subsequently expanded by Wied-Neuwied (1830), who described both sexes, implying that at least two specimens were collected. Although only one of these syntypes remains (Allen 1889; LeCroy 2012), Hoffmann & Geller-Grimm (2013) reported an unsexed adult specimen housed at the Museum Wiesbaden, Wiesbaden, Germany (MWNH 5095), probably since Wied-Neuwied’s lifetime and with no original label preserved, as a potential syntype.

Berlepsch (1911) was the first to point out geographical variation in the Cinnamon Tanager, which was until then treated as monotypic (e.g. Sclater 1886; Ihering & Ihering 1907). In comparison to the nominotypical subspecies, the proposed diagnostic characters of *S. r. capistratus* are its duller, less reddish pileum, paler cinnamon color of the throat and breast, and smaller size, especially tail length (Berlepsch 1911; Hellmayr 1936).

Schistochlamys ruficapillus sicki Pinto & Camargo, 1952, was described from two adult males collected in Chavantina, Rio das Mortes, Mato Grosso, Brazil. The main proposed diagnostic character of this taxon is its smaller size, because its plumage was originally described as indistinguishable from that of the nominotypical subspecies (Pinto & Camargo 1952). Therefore, the assertion of Hilty (2011) that this subspecies is “generally richer and slightly darker in colour tone” is incorrect.

Material and methods

We investigated two taxonomic hypotheses derived from the literature (Hellmayr 1936; Pinto and Camargo 1952): 1) Three distinct taxa are identifiable, each associated with a distinct biogeographic province (Atlantic Forest, Caatinga, and Cerrado), and 2) Body size and plumage coloration vary clinally, with larger and more richly colored individuals at southern sites, and smaller and paler birds at northern sites.

We analyzed 357 specimens housed at the following institutions: American Museum of Natural History, New York, USA (AMNH); Academy of Natural Sciences of Philadelphia, Philadelphia, USA (ANSP); Natural History Museum, Tring, UK (BMNH); Coleção Ornitológica Marcelo Bagno da Universidade de Brasília, Brasília, Brazil (COMB); Departamento de Zoologia da Universidade Federal de Minas Gerais, Belo Horizonte, Brazil (DZUFMG); Field Museum, Chicago, USA (FMNH); Louisiana State University Museum of Natural Science, Baton Rouge, USA (LSUMZ); Museu de Biologia Professor Mello Leitão, Santa Teresa, Brazil (MBML); Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte, Brazil (MCNA); Muséum National d’Histoire Naturelle, Paris, France (MNHN); Museu Nacional, Rio de Janeiro, Brazil (MNRJ); Museu Paraense Emílio Goeldi, Belém, Brazil (MPEG); Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP); Naturhistorisches Museum, Vienna, Austria (NMW); Naturhistoriska Riksmuseet Stockholm, Sweden (NRM); Reserva Ecológica do Instituto Brasileiro de Geografia e Estatística, Brasília, Brazil (RECOR); Senckenberg Naturmuseum, Frankfurt, Germany (SMF); Universidade Federal de Mato Grosso, Cuiabá, Brazil (UFMT); National Museum of Natural History, Washington, DC, USA (USNM); Museum für Naturkunde, Berlin, Germany (ZMB) and Zoologische Staatssammlungen Museum, Munich, Germany (ZSM). These collections house the type specimens of all names available for the Cinnamon Tanager: *Saltator ruficapillus* Vieillot, 1817 (MNHN 7093.2010), *Tanagra leucophaea* Lichtenstein, 1823 (ZMB 5730), *Tanagra capistrata* Wied-Neuwied, 1821 (AMNH 6861) and *Schistochlamys ruficapillus sicki* Pinto & Camargo, 1952 (MZUSP 32617). The alleged holotype of *Tanagra capistrata* Spix, 1825, was also examined (ZSM A1471).

We used a dial caliper to measure (to nearest 0.1 mm) the lengths of total culmen, closed wing (chord), tail and tarsus (Baldwin *et al.* 1931). In addition, to evaluate Hellmayr’s (1936) statement that the tail of *S. r. capistratus* is disproportionately shorter than that of *S. r. ruficapillus*, we computed the dimensionless variable tail length/wing length (TL/WL). We did not include specimens showing signs of immaturity, such as dusky lores, pale buff-yellow chest, and dorsal feathers brownish or washed green (Isler & Isler 1987; Willis & Oniki 2003; Hilty 2011).

We used a simple hybrid index (Sibley & Short 1959) to score all specimens examined for the two main plumage characters considered diagnostic of subspecies, the color of the throat and breast, and the color of the pileum. Although we tried an index with more variables, we found that these two were sufficient to summarize the main proposed diagnostic characters. It is important to remember that, according to Pinto & Camargo (1952, 1957), *S. r. sicki* is “very similar” in plumage color to the nominotypical subspecies, and that these two subspecies can be distinguished by measurements only (*contra* Hilty 2011). Color names and notations follow Munsell (2000), although no color available in this catalogue closely matched the color of the specimens examined, especially the color of throat and breast; nonetheless, it was useful for comparing specimens housed in different collections.

The color of the throat and breast was scored 0 if brownish yellow (color 10YR 6/6 of the Munsell Catalogue) as in typical *S. r. ruficapillus* (and consequently in *S. r. sicki*, which is acknowledged as indistinguishable based on plumage characters), 2 if very pale brown (10YR 7/4) as in *S. r. capistratus*, and 1 if intermediate. The color of the pileum was scored 0 if brown or dark yellowish brown (10YR 4/3 or 10YR 4/4, respectively) as in typical *S. r.*

ruficapillus, 2 if very dark grayish brown or dark grayish brown (10YR 3/2 or 10YR 4/2) as in *S. r. capistratus*, and 1 if intermediate. These standard colors were scored from toptypical or almost toptypical recently collected specimens with fresh plumage. This was necessary because plumage coloration might change slightly with wear and aging of specimens, becoming paler in older faded ones or in those with the plumage severely worn (pers. obs.). To avoid such bias, specimens that exhibited any of these conditions were not included in the analysis.

The two scores were summed as a measure of plumage coloration. Therefore, specimens that were typical *S. r. ruficapillus* (and *S. r. sicki*) scored 0, those typical *S. r. capistratus* scored 4, and intermediate birds scored 1–3. Although this method is admittedly crude and subjective for evaluating plumage states that vary in a continuous way, it allows a simple and quick analysis of the geographical pattern of variation when scores are plotted on a map.

For some of the morphometric analyses it was necessary to refer available specimens *a priori* to one of the currently recognized subspecies. Given that the diagnosis of *S. r. sicki* is based exclusively on body measurements and that there are reports of specimens intermediate between *S. r. ruficapillus* and *S. r. capistratus* (Pinto & Camargo 1952, 1957), which makes identification of the subspecies based only on morphology somewhat awkward, identification to subspecies level was based exclusively on geographic distribution. Therefore, we assumed that these taxa are allopatric, or, at most, parapatric, excluding the possibility of sympatry.

We adopted the following geographic limits, based on previous morphological data (Hellmayr 1929, 1936; Pinto 1944; Pinto & Camargo 1952; Pinto 1954; Storer 1970; Lopes *et al.* 2009): 1) *S. r. ruficapillus*—states of Minas Gerais (south of 19°50'S), Espírito Santo, Rio de Janeiro, São Paulo, Mato Grosso do Sul, and Paraná, in areas dominated by Atlantic Forest and its ecotonal areas with the Cerrado; 2) *S. r. capistratus*—all states in northeastern Brazil plus northern Minas Gerais (north of 15°00'S, which encompasses the type locality [15°06'S, 41°41'W] of this taxon according to Paynter & T aylor 1991)—this region is covered predominantly by Caatinga vegetation (mainly low and dry shrub forests); 3) *S. r. sicki*—states of Mato Grosso and Pará, as well as the states of Goiás and Tocantins in the watersheds of Amazonian rivers—this region is covered by Cerrado vegetation and its ecotonal areas with the Amazon forest. Birds collected in intervening areas were not referred to any subspecies because they might represent intergrades.

The diagnosability of the subspecies of Cinnamon Tanager was assessed by the method proposed by Patten & Unitt (2002), at a diagnosability level of 95%. Specimens collected in possible zones of intergradation were not included in the analyses because they could hamper the diagnosability of subspecies (Remsen 2010).

Data on habitat use and geographic distribution of this species were compiled after extensive literature review, examination of museum specimens and twelve years of intermittent fieldwork over its entire range (see Lopes & Gonzaga 2014).

Statistical analysis. We investigated the existence of significant differences in body measurements between subspecies using a one-way ANOVA, followed by a Tukey test for *a posteriori* comparisons (Zar 2010). We compared the TL/WL ratio of *S. r. ruficapillus* and *S. r. capistratus* by Student's *t*-test, after the log-transformation of this variable. This procedure allows the application of linear statistical methods, avoiding problems associated with the statistical analysis of ratios (Baur & Leuenberger 2011).

We also conducted a Principal Component Analysis (PCA) with varimax rotation, a technique that summarizes patterns of correlations among observed variables, reducing a large number of variables to a smaller number of components (Tabachnick & Fidell 2007). Variables used in the PCA were the lengths of closed wing chord, tail, tarsus, and total culmen.

We investigated the hypothesis of clinal variation in body size taking into account Bergmann's Rule (Rensch 1938; James 1970), the "tendency of organisms to be smaller at high temperatures and low latitudes and larger at low temperatures and high latitudes" (Meiri 2011). Therefore, we considered two variables: latitude and elevation. Bergmann's Rule is not a law but instead a general pattern exhibited by many taxa (Zink & Remsen 1986; Blackburn *et al.* 1999; Meiri *et al.* 2007). We used multiple regression (Zar 2010) to describe the relationship between body size (measured as the first principal component scores, PC1; Zink & Remsen 1986) and latitude and elevation of the collection site. For all analyses we used the software STATISTICA 8.0 (StatSoft 2007). Significance level adopted was 5%.

Results

Our data revealed major extensions of the species' range (Figure 1), which show that *S. ruficapillus* occurs over almost all Brazilian territory outside of Amazonia. Records that represent range extensions of 300–900 km were obtained from the states of Pará (AMNH 431590, 431591, MPEG 15032, 34351–55), Tocantins (MNHN 529.1968, 531.1968, MPEG 20681, MZUSP 53106, 53107, 70442), Mato Grosso (COMB 678, 679 and UFMT 1941, 1943), and Mato Grosso do Sul (AMNH 319636–38, MZUSP 64118, 64119). The exact localities of these noteworthy records are presented in the Appendix I. Specimens were collected from sea level to as high as ca. 2,350 m, in Casa Queimada, Serra do Caparaó (AMNH 317174, 317175).

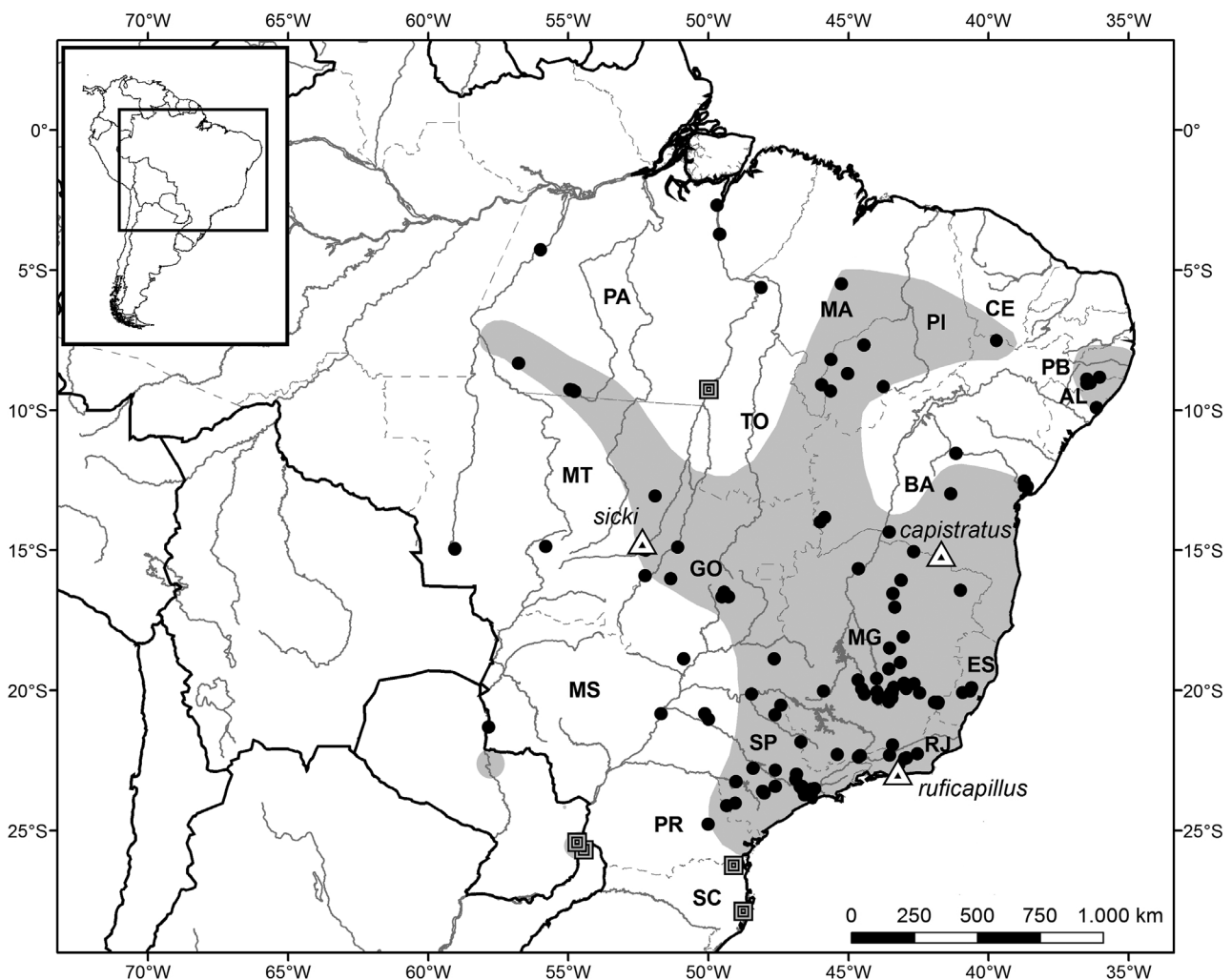


FIGURE 1. Geographic distribution of *Schistochlamys ruficapillus* based on examined specimens (black dots) and some noteworthy literature records (squares) (Rosário 1996; Barnett & Pearman 2001; Zapata 2003; Pinheiro & Dornas 2009). Triangles indicate the type localities of *Schistochlamys ruficapillus sicki* Pinto & Camargo, 1952, *Tanagra capistrata* Wied-Neuwied, 1821, and *Saltator ruficapillus* Vieillot, 1817. Gray shading indicates the species' range according to Ridgely & Tudor (2009). Brazilian states are indicated as follows: AL—Alagoas, BA—Bahia, CE—Ceará, ES—Espírito Santo, GO—Goiás, MA—Maranhão, MG—Minas Gerais, MT—Mato Grosso, MS—Mato Grosso do Sul, SP—São Paulo, TO—Tocantins, PA—Pará, PB—Paraíba, PI—Piauí, PR—Paraná, RJ—Rio de Janeiro, SC—Santa Catarina.

The Cinnamon Tanager inhabits a wide spectrum of semi-open habitats. In the Atlantic Forest region this species is uncommon to fairly common at forest borders and in young second growth at lower elevations (pers. obs.), and common above treeline (Vasconcelos & Rodrigues 2010; pers. obs.), where it inhabits the *campos de altitude*, a cool-humid, grass-dominated formation restricted to highlands (Safford 1999). This species is also found at sea level in coastal *restinga* vegetation (Lima Neto & Lima 2005; Gomes *et al.* 2008). In the Cerrado region of central Brazil, this species is found locally in low and dense shrub savanna areas. It is particularly common in the

highlands of the Espinhaço Range (above 1,000 m), where it inhabits *campo rupestre* (Vasconcelos & Rodrigues 2010), a shrubby grassland rich in endemic plant species that grows on rock outcrops (Giulietti *et al.* 1997). In the northeastern Caatinga region this species is usually found in areas covered by dense scrub and low trees, locally known as *carrasco*. In the Amazon region this species also inhabits the borders or more open patches of *campinarana* (Pacheco & Olmos 2005), a low, evergreen, sclerophyllous forest growing on white-sand soils.

Males of the three subspecies average larger than females, especially in wing and tail length (Table 1). Nevertheless, measurements overlap broadly and specimens cannot be sexed by measurements.

TABLE 1. Morphometric characters and statistical comparisons between subspecies of *Schistochlamys ruficapillus*. Juvenile specimens were excluded. All linear measurements in mm, presented as means \pm standard deviation (SD), followed by sample size and minimum-maximum values.

Character	Sex	<i>S. r. ruficapillus</i>				<i>S. r. capistratus</i>			
		Mean	SD	n	Min-Max	Mean	SD	n	Min-Max
Wing length	♂	83.5A*	2.74	67	77.5–89.1	78.3B*	4.06	32	70.4–84.8
	♀	80.9A	2.73	51	75.5–87.2	75.7B	3.56	28	68.9–81.8
Tail length	♂	81.7A*	2.88	67	76.9–89.5	76.6B	4.00	30	69.0–83.8
	♀	78.9A	3.07	51	72.5–86.0	74.6B	4.76	28	66.1–82.1
Tarsus length	♂	24.3A	1.17	67	21.8–26.8	23.4B	1.18	30	21.1–25.7
	♀	24.5A	1.00	51	22.7–26.4	23.1B	1.58	28	20.4–26.4
Culmen length	♂	17.5A	0.83	66	15.7–19.2	17.5AB	0.91	32	15.4–19.0
	♀	17.5A	0.96	49	15.6–19.5	17.3AB	0.81	28	15.3–18.9
Weight	♂	36.9	5.43	8	26.0–42.5	25.6	6.52	4	20.5–35.0
	♀	37.3	4.70	9	30.8–45.0	25.8	4.32	7	20.5–33.0

continued.

Character	Sex	<i>S. r. sicki</i>			
		Mean	SD	n	Min-Max
Wing length	♂	75.0C*	3.38	17	70.3–80.8
	♀	70.4C	2.44	18	66.1–78.1
Tail length	♂	71.3C*	3.61	17	64.9–78.0
	♀	68.0C	2.40	18	63.1–73.6
Tarsus length	♂	22.7B*	1.01	17	20.5–24.9
	♀	21.9C	0.68	18	20.5–23.0
Culmen length	♂	16.9B	1.00	17	15.0–18.0
	♀	16.7B	0.77	18	15.5–18.4
Weight	♂	30.4	3.50	5	25.2–35.0
	♀	28.7	4.73	3	25.0–34.0

*The superscript asterisk indicates that males differ significantly from females of the same subspecies. Means followed by different capital letters in the same line differ significantly. We did not perform any statistical test for body weight because, in addition to the small sample size, this variable has a substantial non-geographical component generally (Zink & Remsen 1986).

We confirmed predicted differences in body size among subspecies, with *S. r. ruficapillus* the largest one, followed by *S. r. capistratus* and then *S. r. sicki* (Table 1). However, we verified a broad overlap in body measurements of *S. r. ruficapillus* and *S. r. capistratus*, as well as between *S. r. capistratus* and *S. r. sicki*. Overlap in body measurements of *S. r. ruficapillus* and *S. r. sicki* is negligible (Table 1).

No subspecies was diagnosable at a 95% level (Table 2) based on morphometric characters. When a more flexible level of 75% (“Amadon’s rule”) was adopted (Patten & Unitt 2002), only females of *S. r. sicki* and females of *S. r. ruficapillus* were consistently diagnosable from each other, though neither of these differs from *capistratus*.

TABLE 2. Diagnosability of subspecies of *Schistochlamys ruficapillus* based on the pairwise diagnosability index (Patten & Unitt 2002) calculated from PC1 factor scores (used as a measure of body size). Values for males are presented above the diagonal, and those for females below. Negative values indicate that the subspecies are not diagnosable at a 95% level.

Taxon	<i>S. r. ruficapillus</i>	<i>S. r. capistratus</i>	<i>S. r. sicki</i>
<i>S. r. ruficapillus</i>	-	$D_{rc} = -1.91$; $D_{cr} = -1.75$	$D_{rs} = -0.88$; $D_{sr} = -0.78$
<i>S. r. capistratus</i>	$D_{cr} = -1.72$; $D_{rc} = -1.91$	-	$D_{cs} = -2.37$; $D_{sc} = -2.42$
<i>S. r. sicki</i>	$D_{sr} = -0.22$; $D_{rs} = -0.21$	$D_{sc} = -1.86$; $D_{cs} = -1.66$	-

We found no significant differences in TL/WL between males ($df = 95$, t -value = -0.266 , $p = 0.79$) or females ($df = 77$, t -value = -1.364 , $p = 0.18$) of *S. r. ruficapillus* and *S. r. capistratus*. The PCA revealed no clear-cut separation between currently recognized subspecies, and several specimens are intermediate (Figure 2). The contribution ratios of the first principal component (PC1) were 60.9% for males and 68.6% for females. The second principal component (PC2) contributed with 22.0% and 20.2%, respectively. PC1 represents a relationship among body size measurements, especially wing (factor loadings of 0.87 for males and 0.86 for females), tail (0.85 and 0.83) and tarsus lengths (0.81 and 0.91), while PC2 represents the culmen length (0.94 and 0.96), which was not strictly correlated with other body measurements.

The multiple regression analysis revealed a highly significant association between body size and the latitude and elevation of the collection site ($p < 0.00001$ for males and females). Nevertheless, the model explained just about half of the variability in body size for males ($n = 132$; $R^2 = 0.45$), with latitude explaining a larger part of the variation ($\beta = 0.5783$, $SE = 0.072$) than elevation ($\beta = 0.1745$, $SE = 0.072$). A similar pattern was obtained for females ($n = 109$; $R^2 = 0.52$; $\beta = 0.6165$, $SE = 0.075$; $\beta = 0.1900$, $SE = 0.075$, respectively). Although data on body weight are scarce for this species, the pattern of variation seems similar, with some male specimens of *S. r. ruficapillus* almost 70% heavier than those of *S. r. sicki* (Fry 1970; see Table 1).

Figure 3 reveals a complex pattern of body size variation, which cannot be described as a simple linear cline. Smaller birds occur in the central-western portion of the species' range, specifically in northern Mato Grosso and southern Pará. Larger birds occur at southern and southeastern sites, and intermediate individuals occur in the northeastern and central-southern portions of its range. Males and females found in the extreme north of the range are on average larger than those found in the central-western portion.

Individual variation in plumage coloration of the three subspecies is substantial, and the pattern of geographical variation is equally complex (Figures 4 and 5). Again, subspecies cannot be diagnosed on the basis of plumage coloration; a simple counting of plumage states (Table 3) reveals that no subspecies achieves the 95% level of diagnosability. Birds from the states of Paraná, Mato Grosso do Sul, São Paulo, Rio de Janeiro and Espírito Santo show the typical, or near-typical, plumage of *S. r. ruficapillus* (hybrid index 0 or 1; Figure 4). Specimens from central Minas Gerais are highly variable, with hybrid indices ranging from 0 to 4. Specimens from northern Minas Gerais and coastal northeastern Brazil (states of Bahia, Alagoas, and Pernambuco) are typical or near-typical *S. r. capistratus* (hybrid index 4 or 3; Figure 4). Specimens from Piauí are also highly variable.

TABLE 3. Hybrid index based on plumage coloration for 261 specimens of *Schistochlamys ruficapillus*. Specimens which scored 0 represent typical *S. r. ruficapillus* (and *S. r. sicki*, which are allegedly indistinguishable in plumage coloration). Specimens which scored 4 represent typical *S. r. capistratus*. Specimens scored 1-3 represent intermediate specimens.

Taxon	Hybrid index					n
	0	1	2	3	4	
<i>S. r. ruficapillus</i>	88	19	9	8	0	124
<i>S. r. capistratus</i>	2	7	12	17	25	63
<i>S. r. sicki</i>	20	7	7	3	4	41
"Intergrades"	9	1	10	9	4	33

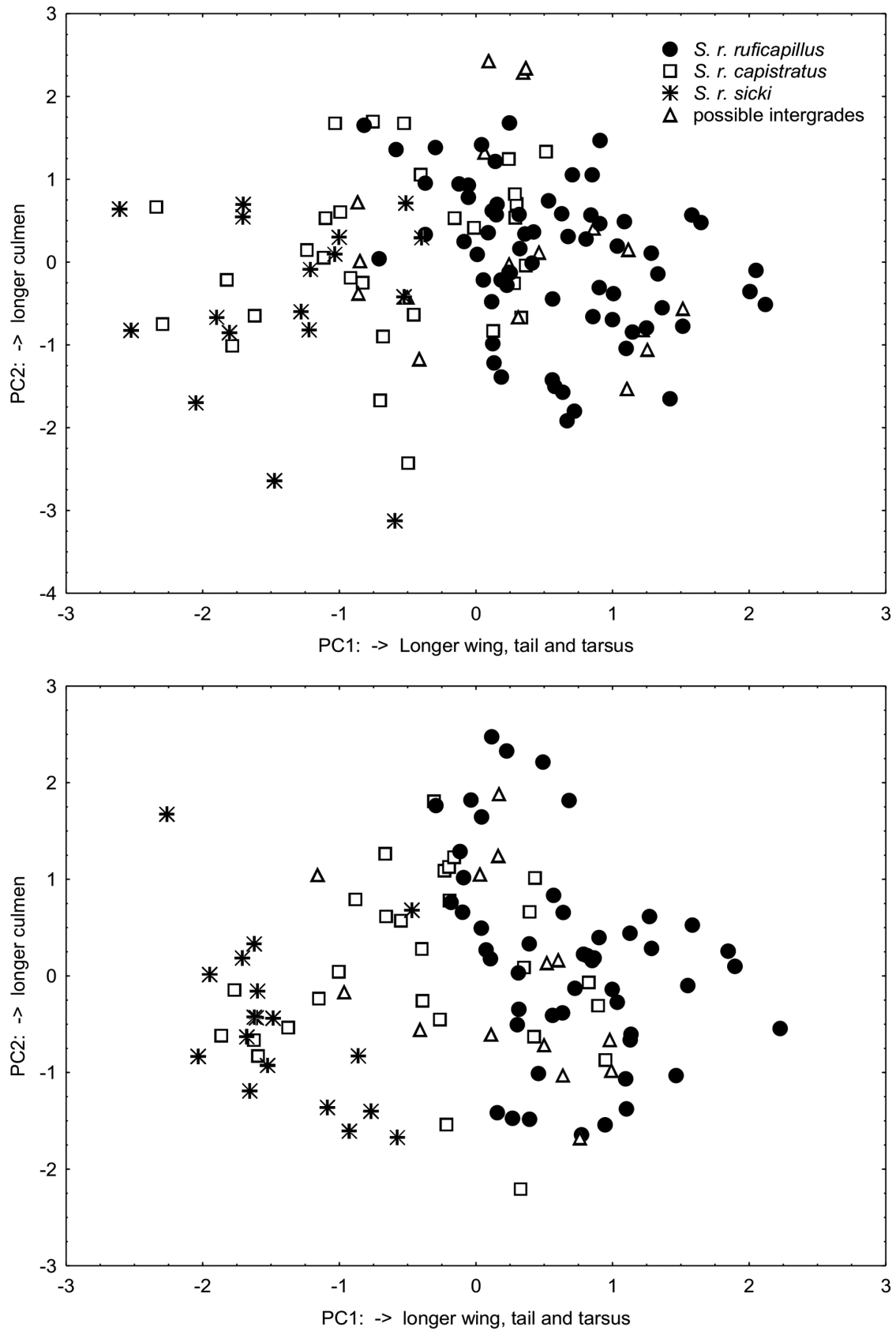


FIGURE 2. Scatterplots of the first versus the second principal component scores of a Principal Component Analysis of morphometric variables measured from specimens of *Schistochlamys ruficapillus*. Males above ($n = 132$) and females below ($n = 109$).

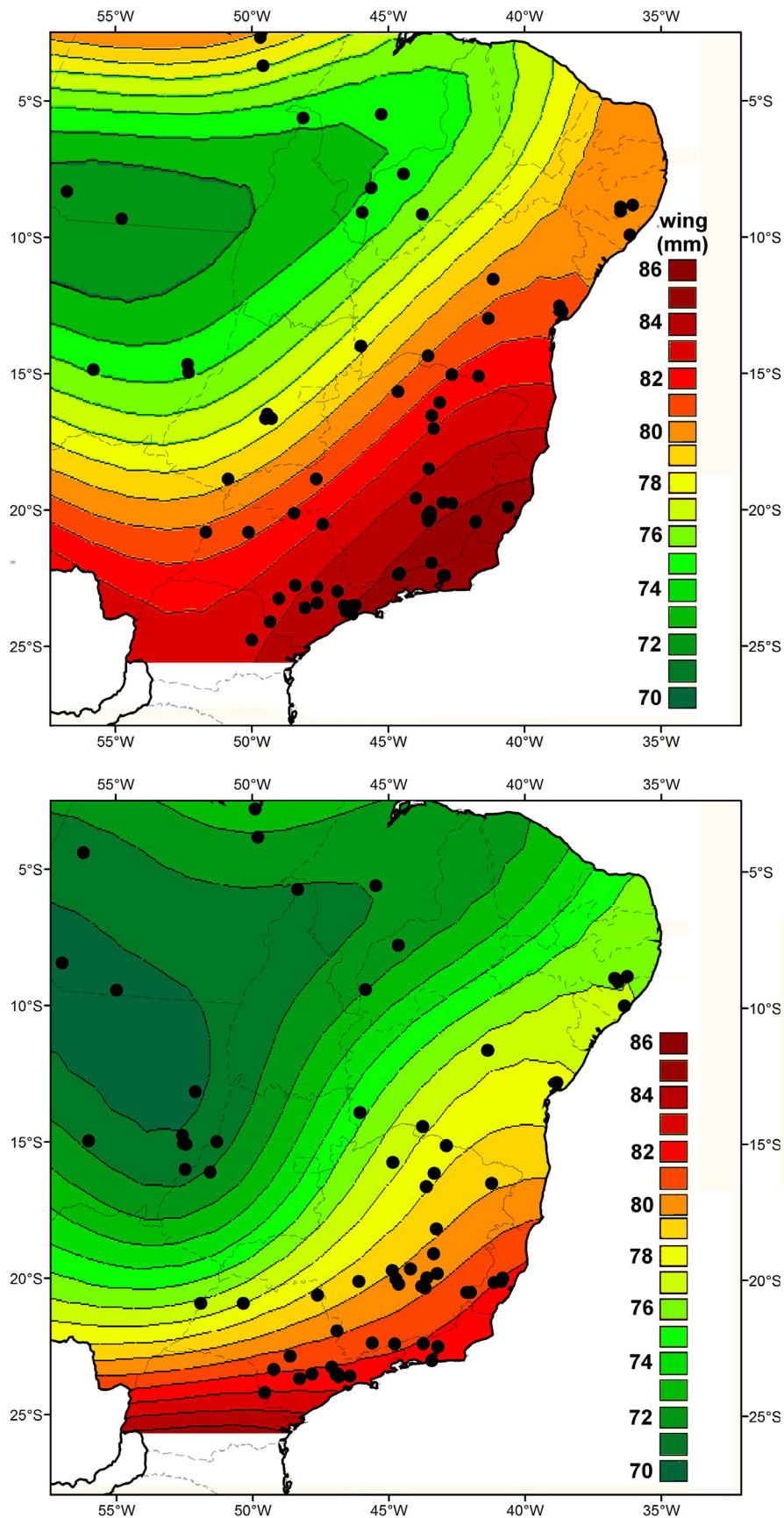


FIGURE 3. Contour plot (Distance-Weighted Least Squares Fitting) depicting geographic distribution of wing length variation in *Schistochlamys ruficapillus*. Males above (n = 135) and females below (n = 111). Black dots indicate the location of samples available.

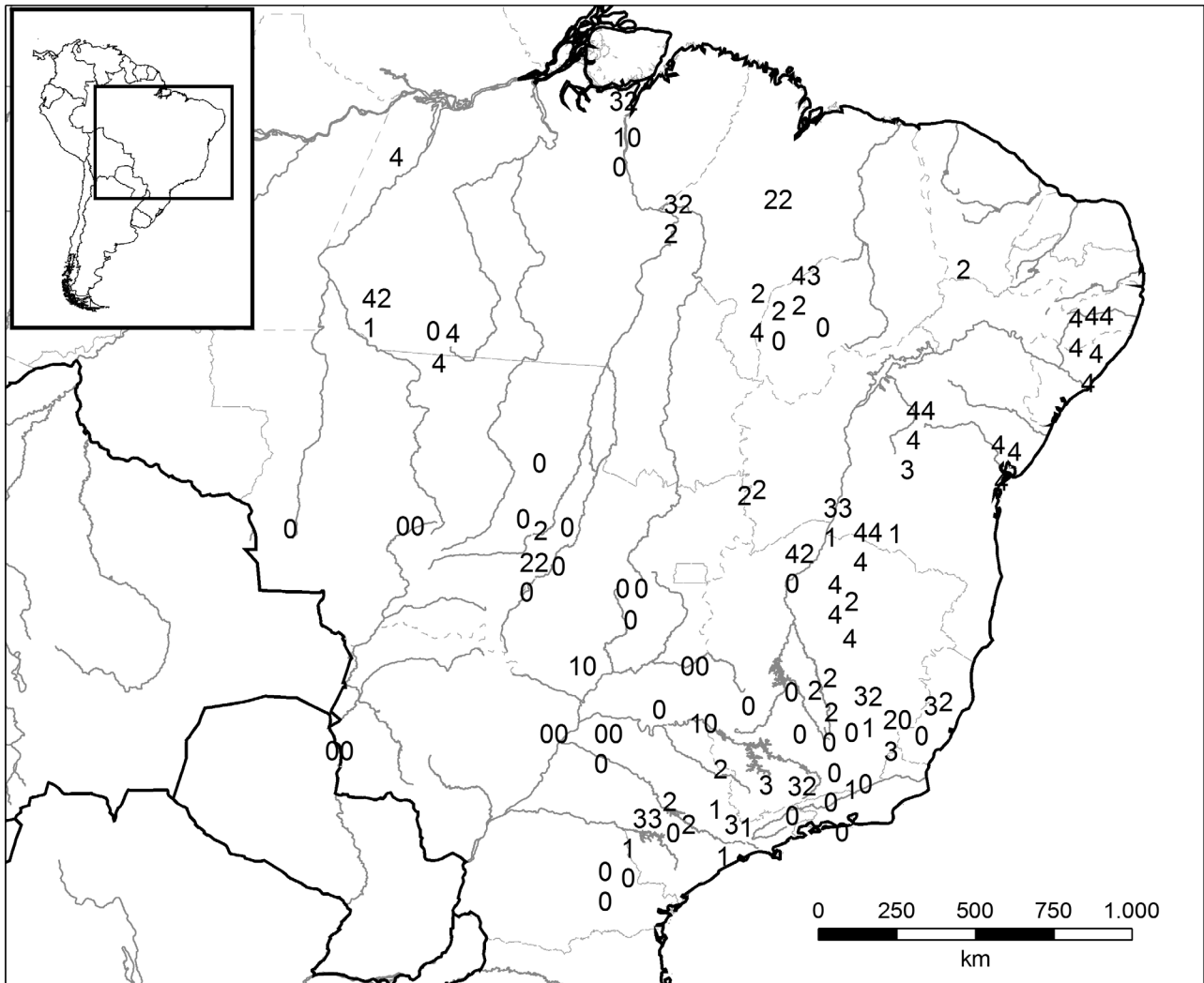


FIGURE 4. Geographic distribution of hybrid index variation in *Schistochlamys ruficapillus*. Values near “zero” refer to the *S. r. ruficapillus* phenotype (also *S. r. sicki*, which is indistinguishable based only on plumage characters), whereas values near “four” refer to the *S. r. capistratus* phenotype.

Birds from central Minas Gerais are intermediate in coloration between typical *S. r. ruficapillus* from Rio de Janeiro and São Paulo and typical *S. r. capistratus* from Bahia, forming a transition zone between these two chromatic extremes. Although series from a single locality are small, among five specimens from Januária (in northern Minas Gerais) we found some that are clearly assignable to either *S. r. ruficapillus* (e.g. DZUFMG 5535) or *S. r. capistratus* (DZUFMG 5536), as well as an intermediate specimen (DZUFMG 5537).

Plumage coloration of specimens from northeastern Brazil is also variable. Birds from near the type locality of *S. r. capistratus* show the typical characters attributed to that subspecies. However, specimens from Piauí and Maranhão are small, similar to *S. r. sicki* in size, but their plumage coloration is highly variable, with some birds approaching typical *S. r. ruficapillus*, and others, typical *S. r. capistratus*.

Measurements of the extant syntype of *S. r. capistratus*, which is a male, are typical of northeastern Brazilian specimens (wing 78.4, tail 76.7, tarsus 22.2 and culmen 17.6; see Table 1), but its plumage coloration approaches that of southern birds. This specimen, in remarkably good condition after almost 200 years, is slightly faded, which makes determination of its original colors difficult (see Hoffmann & Geller-Grimm [2013] for a color photograph of another potential syntype housed in MWNH). Nevertheless, the color of its throat and breast (between 10YR 6/4 and 6/6), as well as of its pileum (between 10YR 4/2 and 3/2), closely approaches that of toptotypical *S. r. ruficapillus*. We propose that the alleged paler coloration of *S. r. capistratus* described by Berlepsch (1911), and reiterated by all subsequent authors, was based not on the plumage coloration of the syntype, but rather on the examination of Bahia trade skins, which were numerous in European collections at that time.



FIGURE 5. Examples of size and color variation in *Schistochlamys ruficapillus*. We present the hybrid index (hi) of each specimen followed by its component scores (the color of the throat and breast and the color of the pileum, respectively) enclosed in square brackets. From left to right, *S. r. capistratus* from Bahia (MZUSP 27723; hi = 3 [1, 2]), *S. r. sicki* from Mato Grosso (MZUSP 35302; hi = 1 [1,0]), *S. r. sicki* from Mato Grosso (MZUSP 32617 [holotype]; hi = 0 [0, 0]), *S. r. ruficapillus* from Paraná (MZUSP 6906; hi = 0 [0, 0]), *S. r. ruficapillus* from São Paulo (MZUSP 34623; hi = 0 [0, 0]), *S. r. capistratus* from Alagoas (MZUSP 39259; hi = 4 [2, 2]), and *S. r. capistratus* from Piauí (MZUSP 75409; hi = 0 [0, 0]). Note marked geographical and individual variation.

Although the color of the throat and breast and the color of the pileum of the holotype of *S. r. sicki* are indistinguishable from those of specimens from the range of *S. r. ruficapillus*, these specimens vary widely in these characters. Two other specimens referred by Pinto & Camargo (1952) to *S. r. sicki* (MZUSP 32618 and 35302) are almost indistinguishable from the smaller specimens of *S. r. capistratus*, such as the two females collected in Ilha Madre de Deus, coastal Bahia (MZUSP 14353 and 27723). We must also stress that the central rectrices of the holotype of *S. r. sicki* were molting, thus emphasizing its small size.

Birds collected in the range of *S. r. sicki* are also not uniform in plumage coloration (Figure 6). Specimens from Goiás and Mato Grosso are similar to those of the nominotypical subspecies, whereas birds from northern Tocantins and Pará encompass the species' full range of variation in color (hybrid indices ranging from 0 to 4). Some specimens from the range of *S. r. sicki* are large and dark (e.g. MPEG 34354), whereas others are small and pale (e.g. MZUSP 38598). In a similar way, specimens referred to *S. r. capistratus* are not uniform; some specimens are large and pale (e.g. AMNH 245702), whereas others are small and dark (e.g. MZUSP 75409).

Therefore, variation in body size is not closely associated with variation in plumage coloration, and a simple linear cline does not accurately describe the morphological variation observed in this species.



FIGURE 6. Examples of color variation in *Schistochlamys r. sicki*. We present the hybrid index (hi) of each specimen followed by its component scores (the color of the throat and breast and the color of the pileum, respectively) enclosed in square brackets. From left to right, specimens from southern Pará (MZUSP 38599; hi = 4 [2, 2]), eastern Mato Grosso (MZUSP 35302; hi = 1 [1, 0]), eastern Mato Grosso (MZUSP 32617 [holotype]; hi = 0 [0, 0]), northern Tocantins (MZUSP 53107; hi = 3 [1, 2]), southern Pará (MZUSP 38598; hi = 4 [2, 2]), and northern Tocantins (MZUSP 70442; hi = 2 [2, 0]). Note marked geographical and individual variation.

Discussion

Schistochlamys ruficapillus has a geographic distribution much wider than is depicted in available field guides and handbooks (e.g. Isler & Isler 1987; Ridgely & Tudor 2009; Hilty 2011). The range extensions presented here cannot be attributed to man-made environmental disruptions, because these records are based on birds collected in relatively well preserved sites that were poorly sampled until quite recently (Silva & Santos 2005), and on old, but overlooked, museum specimens (e.g. AMNH 319636 and MNHN 529.1968).

The species' elevational range is also wide, from sea level to the highest summits (up to 2,350 m) in southeastern Brazil (Vasconcelos & Rodrigues 2010), well above the uppermost limit of 1,100 m usually cited

(Isler & Isler 1987; Stotz *et al.* 1996; Ridgely & Tudor 2009), although Hilty (2011) reported that it occurs up to 1,200 m, locally to 2,050 m.

The Cinnamon Tanager shows substantial morphological variation among populations, both in size and coloration. Individual variation within populations is also significant, but not as great as geographical variation. Nevertheless, diagnosis of the currently accepted subspecies cannot be achieved consistently, because many intermediate individuals do exist, suggesting considerable genetic exchange between populations.

Although the multiple regression showed a significant association between body size and the latitude and elevation of the collection site, much of the variation in body size was not explained by our model. Therefore, Bergmann's rule might not be the only explanation for the complex pattern of body size variation observed. This is because several specimens of *S. r. sicki* collected in central Brazil, in comparison with specimens of *S. r. capistratus* collected at the same latitude and elevation, are unexpectedly small.

The pattern of morphological variation observed, along with our field observations and literature data, lead us to formulate a third hypothesis that remains to be tested. This hypothesis predicts that body size varies in a clinal way, following Bergmann's rule, but that this pattern is obscured in central Brazil by character displacement (Losos 2000; Schluter 2000) promoted by the sympatric occurrence of a larger competing species, the congeneric Black-faced Tanager *S. melanopis*. This hypothesis is based on the observation that the two species of *Schistochlamys* are territorial, with similar diet and habitat requirements (Isler & Isler 1987; Domingues & Rodrigues 2007; Ridgely & Tudor 2009; Hilty 2011), and that agonistic encounters between them have been recorded in central Brazil (Lopes *et al.* 2009), where both species overlap in range (Ridgely & Tudor 2009). Furthermore, the two subspecies of the Black-faced Tanager found across central Brazil (*S. m. olivina* and *S. m. amazonica*) seem to be larger than their counterparts from the remainder of the species' range (with the possible exception of *S. m. grisea*) (Zimmer 1947; Storer 1970).

Losos (2000) summarized six tests for the hypothesis of ecological character displacement, which involve a variety of approaches and techniques. Testing the hypothesis of character displacement between the two species of *Schistochlamys* is a challenging task, because the data at hand are far from suitable. For example, morphological variation in the Black-faced Tanager is poorly understood, and areas of sympatry between these taxa are not well known (Zimmer 1947). Detailed ecological and behavioral data are also lacking. Testing of this hypothesis is therefore required.

In short, *S. ruficapillus* is a highly variable species that shows marked individual and geographical variation in body size and plumage coloration. Diagnosis of the three currently accepted subspecies is not possible, because of extensive sharing of character states among populations of southern/southeastern, northern/central and northeastern Brazil. We conclude that the proposal of three subspecies in *S. ruficapillus* by earlier taxonomists, and their recognition by more recent ones, was due to small sample sizes associated with large gaps in sampling, which made an accurate appreciation of the morphological variation in this species difficult.

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APPENDIX 1. List of the specimens examined.

Small orthographical errors in the names of many localities have been corrected. All specimens were collected in Brazil.

UNSPECIFIED: (6♂—ANSP 7860, 7861, 7862, 7863, 7864, ZMB 14852; 1♀—BMNH 1885.6.12.1087; 24 unsexed—AMNH 4572, 511599, 511600, 511601, 511602, 511603, 511604, 511605, 511606, 511607, 511608, 511609, 511616, 818802, ANSP 64333, BMNH 1905.6.28.216, MNHN 505.1854, 2667.1999, 2668.1999, 2669.1999, 2670.1999, 7093.2010 [Holotype of *Saltator ruficapillus* Vieillot, 1817], SMF 58761, ZMB 5730 [Holotype of *Tanagra leucophaea* Lichtenstein, 1823]). **MARANHÃO:** Alto Parnaíba (2♂—FMNH 63602, 63605); Barra do Corda (2♂—FMNH 63603, 63604; 1♀—FMNH 63601). **PIAUI:** [Barra do Rio] Corrente, Rio Parnaíba (1♂—NMW 69635); Fazenda Ema-Flor, Bom Jesus (3 unsexed—MZUSP 75408, 75409, 75410); Fazenda União, Uruçui (3♂—MPEG 68733, 68734, 68736; 4♀—MPEG 68731, 68732, 68735, 68737); Parque Nacional da Serra das Confusões (1♂—MZUSP 77886); Santa Filomena, Rio Parnaíba

(1♀—NMW 69636). **PERNAMBUCO:** Brejão (2♂—AMNH 245699, 245700); Exu (1 unsexed—MNHN 1013.1971); Garanhuns (2♂—AMNH 245702, 245703, 2♀—AMNH 245701, 245704); [Fazenda] Macuca (1♀—BMNH 1885.6.12.1081); Vista Alegre (1♂—BMNH 1885.6.12.1082, 1♀—BMNH 1885.6.12.1083). **PARÁ:** Alto Rio Cururu, afluyente Tapajós, Cururu (1♀—LSUMZ 32302; 1 unsexed—MPEG 23144); Baião, Rio Tocantins (2♂—AMNH 431590, 431591); Base Aeronáutica, Serra do Cachimbo (1 unsexed—MPEG 57993); Fazenda São Francisco, Serra do Cachimbo, Novo Progresso (1 unsexed—MPEG 57994); Itaituba (1♀—MPEG 15032); PA-263, km 18, Tucuruí (1♀—MPEG 34351); PA-263, km 18, Tucuruí (4♂—MPEG 34352, 34353, 34354, 35355); Rio Cururu (1♂—MNRJ 30865; 1♀—MNRJ 30871); Serra do Cachimbo (1♂—MZUSP 38598; 2♀—MNRJ 30866, 38599). **TOCANTINS:** Araguatins (4♂—MNHN 529.1968, MPEG 20681, MZUSP 53107, 70442; 2♀—MNHN 531.1968, MZUSP 53106). **GOIÁS:** Aragarças, Rio Araguaia (2♀—MPEG 15030, 15031; 1 unsexed—RECOR 608); Fazenda Transwaal, Rio Verde (1♂—MZUSP 26557; 1 unsexed—ANSP 146671); Fazenda Saloba, Montes Claros de Goiás (1♀—DZUFMG 5470); Goiânia (1♂—MNHN 558.1968; 1 unsexed—FMNH 344774); Goianira (1♂—MNHN 530.1968); Leopoldina, Rio Araguaia (1♀—MNRJ 11385); Trindade (1♂—FMNH 344773); Vale dos Sonhos, 90 km de Barra do Garças (1♀—MPEG 23143); Xavantina, Rio das Mortes (1♂—MZUSP 32617 [**Holotype of *Schistochlamys ruficapillus sicki* Pinto & Camargo, 1952**]; 1♀—MNRJ 30870). **MATO GROSSO:** 45 km NNW da sede municipal, MT-385, Jauru (2 unsexed—UFMT 1941, 1943); Acampamento João Lopes, 210 km N Xavantina (1♀—RECOR 609); Pindaíba, Rio das Mortes (1♂—MZUSP 35302; 1♀—MNRJ 30872); Usina Hidrelétrica do Manso (1♂—COMB 679; 1♀—COMB 678). **ALAGOAS:** Usina Sinimbu (5♂—MZUSP 37678, 37682, 37683, 39261, 39262; 5♀—MZUSP 37679, 37680, 37681, 39259, 39260). **BAHIA:** Unspecified locality (24 unsexed—AMNH 41128, ANSP 108940, BMNH 1885.6.8.368, 1885.6.8.369, 1885.6.8.370, 1885.6.12.1084, MNHN 1892.1958, NMW 69632, 69633, 69634, 86903, ZMB 2000/27013, ZSM 1903.2986, 1909.2789, 1909.2790, USNM 44779, 45562, 45563, 46713, 46900, 54263, 115079, 146722, 146723); Fazenda Ilha (1♂—AMNH 6861 [**Syntype of *Tanagra capistrata* Wied-Neuwied, 1821**]); Santo Amaro (1♂—FMNH 49800); 20 km E Cabeceira do Rio Arrojado, Correntina (1♂—MNRJ 38945); 50 km NE Cabeceira do Rio Arrojado, Correntina (1♀—MNRJ 38947); Brejinho das Ametistas, Caetité (1♂—DZUFMG 6069; 2♀—DZUFMG 6070, 6071); Ilha Madre de Deus (2♂ ANSP 128941, MZUSP 14360; 3♀—ANSP 128940, MZUSP 14359, 27723; 1 unsexed—MZUSP 27722); Morro do Chapéu (7♂—AMNH 245685, 245686, 245687, 245688, 245690, 245691, 245689; 6♀—AMNH 245692, 245693, 245694, 245695, 245696, 245697; 1 unsexed—AMNH 245698); Mucugê (1♂—MZUSP 79899). **MINAS GERAIS:** Unspecified locality (1 unsexed—AMNH 511615); Água Suja, Bagagem (2♂—ZSM 1911.1513, 1911.1514); Casa Queimada, Serra do Caparaó (2♂—AMNH 317175, 317174); Cascata (1♀—NMW 69624); Estação de Pesquisa e Desenvolvimento Ambiental de PETI (1♀—DZUFMG 3699); Fazenda Chapéu do Sol, distrito de Saramenha, Ouro Preto (1♂—DZUFMG 6186); Fazenda do Patrimônio, Divinópolis (1♀—MZUSP 11850); Fazenda Pombal, Vargem Grande (1♂—MNRJ 23963); Fazenda Taveira, Mariana (1♂—MNRJ 11381; 1♀—MNRJ 11380); Jardim Canadá, Nova Lima (1 unsexed—MCNA 1489); Maria da Fé (1♀—MZUSP 15988); Pequi (1♀—SMF 84570); Pico do Inficionado, Serra do Caraça (1♂—DZUFMG 2655); Pico do Sol, Serra do Caraça (1♂—DZUFMG 2711); Raul Soares (1 unsexed—FMNH 191708); Serra do Batatal, Ouro Preto (1♂—DZUFMG 2887; 1♀—DZUFMG 2888); Serra do Caraça (2♂—DZUFMG 2208, 2209); Serra do Itatiaiuçu (1♀—MZUSP 56376); Vargem Alegre (1 unsexed—MZUSP 1443); Chapada de Serro, Pedro Lessa (1♂—DZUFMG 2210); Fazenda Boa Esperança, São José da Lagoa (2♂—MZUSP 25733, 25734; 3♀—MZUSP 25730, 25731, 25732); Jequitinhonha (1♀—MNRJ not numbered); Lapa Vermelha, Pedro Leopoldo (1♂—DZUFMG 2207; 1♀—DZUFMG 2206); Parque Estadual do Rio Doce (1♂—DZUFMG 2213); Refúgio da Vida Silvestre Rio Pandeiros, Januária (3♂—DZUFMG 5535, 5536, 7168; 2♀—DZUFMG 5537, 7169); Riacho dos Machados (4♂—MCNA 2910, 2925, 2926, 2927; 3♀—MCNA 2709, 2767, MFV 3652); Serra do Ambrósio, distrito de Pedra Menina, Rio Vermelho (1♀—DZUFMG 5165); Serra do Cipó (2 unsexed—DZUFMG 2211, 2212); Serra do Pau D'Arco, Santo Antônio do Retiro (1♂—DZUFMG 3061; 2♀—DZUFMG 3059, 3060); Serra Resplandecente, Itacambira (1♂—DZUFMG 3908); Sítio Recanto, Grão Mogol (3♂—DZUFMG 3728, 3729, 3829; 2♀—DZUFMG 3539, 3828); West of Boa Esperança, Serra do Caparaó (1♀—AMNH 317176). **ESPÍRITO SANTO:** Chaves, Santa Leopoldina (1♀—MZUSP 28382); Estação Biológica de Santa Lúcia, Santa Teresa (1♀—MBML 7020); Fazenda do Elveresto, Serra do Caparaó (1♀—MNRJ 12616); Jatiboca (1♀—MNRJ 26977); Santa Teresa (9♂—DZUFMG 2197, 2198, 2200, MBML 6067, 6069, 6071, 6670, MNRJ 19698, 20473; 6♀—DZUFMG 2119, 2199, MBML 6066, 6068, 6070, MNRJ 19699); Serra do Caparaó (2♂—MNRJ 26004, 26087). **RIO DE JANEIRO:** Unspecified locality (6 unsexed—AMNH 511614, 131063, BMNH 1885.6.12.1085, 1895.4.1.122, ZMB 2000/27012, ZSM A1471); Campestre, Nova Friburgo (1♀—MNRJ 38321); Fazenda Alpina (1♂—MNRJ 8790); Km 3 Estrada Nova Friburgo, Teresópolis (1♀—MNRJ 35965); Mirante Dona Marta, Rio de Janeiro (1♀—MNRJ 31654); Monte Serrat, Serra do Itatiaia (2♂—AMNH 189392, 189394; 1♀—AMNH 189393; 1 unsexed—AMNH 189395); Nova Friburgo (1 unsexed—BMNH 1885.6.8.341); Serra do Itatiaia (1♂—MZUSP 36190); Teresópolis (4♂—FMNH 65268, 65270, MNRJ 8766, 8786; 5♀—FMNH 65269, MNRJ 8789, 28003, MZUSP 33847, 33848; 1 unsexed—MNRJ 8791). **SÃO PAULO:** Unspecified locality (1 unsexed—BMNH 1885.6.8.372); Batatais (1 unsexed—MZUSP 1735); Cuca, Horto Florestal (1♀—MZUSP 24747); Emas, São Paulo (2♂—MZUSP 34623, 59775; 1♀—MZUSP 59774); Fazenda Florestal, Itapetininga (1♂—MZUSP 64556); Fazenda Nova (1♂—NMW 69625); Fazenda Santa Madalena, Avaré (5♂—MZUSP 54072, 54073, 54077, 54078, 54079; 4♀—MZUSP 54074, 54075, 54076, 54080); Fazenda Santa Rosa, Ribeirão Paraúna (2♂—MZUSP 23811, 23812; 1♀—MZUSP 23813); Floresta Estadual de Itapetininga (1♂—MZUSP 64398); Franca (1♂—MZUSP 7936; 1♀—MZUSP 7938); Ipanema (5♂—BMNH 1904.7.8.78, NMW 42821, 69629, 69630, ZSM not numbered; 3♀—NMW 69627, 69628, not numbered); Ipiranga (1♂—MZUSP 5639; 1♀—MZUSP 8); Itapetininga (6♂—DZUFMG 2201, 2203, LSUMZ 53119, 53121, 63111, MZUSP 11922; 4♀—DZUFMG 2202, LSUMZ 53120, 63110, MZUSP 11923); Itararé

(2♂—MZUSP 11757, 11927; 4♀—MZUSP 11741, 11747, 11772, 11925); Itatiba (2♂—MZUSP 8810, 14527; 1 unsexed—MZUSP 86); Jundiaí (1♀—MZUSP 878); Mogi das Cruzes (2♂—MZUSP 13914, 29521; 1♀—13917); Paranapiacaba (1♂—FMNH 278293); Rio das Pedras, Ituverava (1♂—MZUSP 3088); Rio Sapucaí (1♂—NMW 69626); São Bernardo [do Campo] (2♂—MZUSP 51218, 56375; 1 unsexed—NMW not numbered); São Jerônimo, Tietê (1 unsexed—MZUSP 4357); Serra da Cantareira (1♀—MZUSP 61003); Suzano (1♂—DZUFMG 2205; 1 unsexed—DZUFMG 2204); Vila Oliveira, Mogi das Cruzes (1♂—MZUSP 29522); Vila Vitoriana, Botucatu [= Victoria] (4♂—AMNH 511610, 511611, 511613, FMNH 49807; 1♀—AMNH 511612). **MATO GROSSO DO SUL:** Fazenda Yamaguti, Três Lagoas (1♂—MZUSP 64118; 1♀—MZUSP 64119); São Francisco Ranch, Campanário (2♂—AMNH 319636, 319637; 1♀—AMNH 319638). **PARANÁ:** Castro: (2♂—AMNH 140167, MZUSP 6906).

UNACCEPTABLE LOCALITIES: GOIÁS: Rio Claro (1♂—BMNH 1885.6.8.374) [Error! = Bahia trade skin]. RIO GRANDE DO SUL: Pelotas (1 unsexed—BMNH 1885.6.8.373) [Error! There is no reliable record of this species for Rio Grande do Sul (Bencke 2001). This is a mislabeled specimen, like many others from Pelotas that were originally deposited in Joyner's collection (see Ihering 1899)].