



A new species of tanager (Aves: Thraupidae) from the Eastern slopes of the Andes

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Abstract

The Black-goggled Tanager (*Trichothraupis melanops*) is a South American forest species that comprises two disjunct populations in the Atlantic Forest and in the Andes. During visits to natural history museums, we noticed morphological differences between these populations, which led to a taxonomic revision of the species based on plumage patterns and morphometry. Our analyses revealed that both populations are fully diagnosable, and that the Andean population represents an undescribed taxon, which we name *Trichothraupis griseonota* **sp. nov.** The new taxon differs from *T. melanops* by the extension of black in the faces of the males, covering the auricular region, and a greyer shade on the back (instead of olive). A previous mtDNA study with *Trichothraupis* is consistent with our conclusions that a new taxon requires recognition. The new species is found from 400 m up to 1,700 m on the eastern slopes of the Andes in Peru, Bolivia, and northwestern Argentina, inhabiting Tucumano-Boliviano and Yungas Forests as opposed to the Atlantic Forests where *T. melanops* is found. The biogeographical disjunction of the two species is similar to what has been observed for other bird species and subspecies, whereby avian lineages are allopatrically distributed and separated by the Chaco-Cerrado vegetation. The description of this taxon reinforces the importance of continued studies and analyses of museum specimens, which may yet reveal little-known patterns and undescribed taxa.

Key words: Andean forests, Atlantic Forest, biogeography, taxonomy, *Trichothraupis*

Introduction

After decades of stasis, we have witnessed a steady increase in the number of bird species recognized in the Neotropical region over the last few years (e.g. Whitney & Cohn-Haft 2013; Barnett & Buzzetti 2014; Dickens *et al.* 2021). This increase can be ascribed to three main sources. Most attention should be directed towards field discoveries of previously completely unknown and never-before-collected taxa (Pacheco *et al.* 1996; Lara *et al.* 2012; Seeholzer *et al.* 2012; Buzzetti *et al.* 2013; Cohn-Haft *et al.* 2013; Hilty *et al.* 2013; Whitney *et al.* 2013; Lane *et al.* 2017), often during expeditions to remote and little-explored regions. A second cause for the growth in species numbers is the elevation of subspecies to species following taxonomic reviews (Cadena & Cuervo 2009; Carneiro *et al.* 2012; Silveira *et al.* 2017; Dantas *et al.* 2021), which are related in part to species concepts adopted and taxonomic practices, and do not necessarily involve any actual new discoveries or descriptions of new taxa. A third and often unappreciated cause of increasing species numbers is what can be termed “museum discoveries”,

whereby renewed examinations of specimens already housed in collections reveal undescribed distinct populations that had remained unnoticed or had flown under the radar of ornithologists (O'Neill *et al.* 2011; Repenning & Fontana 2013). Like field discoveries, these cases involve descriptions of new taxa, but like taxonomic reviews, they are based mainly on reanalyses of previously collected specimens rather than on new findings in the field. The purpose of this paper is to report one such museum discovery.

Trichothraupis melanops (Vieillot, 1818) is a monospecific genus found in two disjunct populations, one in the Atlantic Forest of eastern Brazil (Bahia south to Rio Grande do Sul states), northeastern Argentina, and eastern Paraguay, from sea level up to 1,200 m. Normally associated with the Atlantic Forest, there are some isolated populations in the southern Pantanal as well as in the gallery forests of eastern Chaco. A second population can be found on the eastern slopes of the Andes from northern Peru to extreme northwestern Argentina, mainly from 1,000 m to 1,700 m (Isler & Isler 1987; Ridgely & Tudor 1989; Schulenberg *et al.* 2007; Hilty 2011). *Trichothraupis melanops* is a forest-dwelling bird that lives in pairs or in small groups, and feeds on fruit and arthropods, regularly feeding on army ant swarms (Sick 1997; Ridgely & Tudor 2009). It is common in the Atlantic Forest, where it is bold, conspicuous, and easy to observe (Ridgely & Tudor 1989). However, it is less conspicuous in the Andes, where its main habitat consists of drier forests than in the Atlantic regions (Lane *et al.* 2021; G. Cabanne unpubl.).

Trichothraupis melanops (Vieillot, 1818) was originally described as *Muscicapa melanops*, based on Azara's (1802) "*lindo pardo copete amarillo*". There are no known type specimens, but Vieillot gave the type locality as "Paraguay". Azara himself never saw this bird and his account of it was based on information sent to him by his friend Don Pedro Blas Noséda, a priest at the Jesuit mission in San Ignacio Güazú, in southern Paraguay (Azara 1802). Following its description, the Atlantic population of this species has had a mostly uneventful taxonomic history. A current junior synonym, *Tachyphonus quadricolor* Vieillot, 1819, was proposed by Vieillot, who did not perceive its resemblance to his earlier description of *T. melanops*. A northern form, from Arraial da Conquista, Bahia (northeastern Brazil) was then described as *Tanagra auricapilla* Wied, 1821. Other names have been proposed, including *Muscicapa galeata* Lichtenstein, 1823, *Tachyphonus suchii* Swainson, 1826, and Cabanis (1850) proposed the new combination *Trichothraupis quadricolor*. Based on its paler crest, extensive black on the forehead, olive-grey back and paler underside, Hellmayr validated the northern taxon as the subspecies *T. m. auricapilla* (Wied, 1821), whose female specimen from Espírito Santo, Brazil, was clearly in accordance with the one from Bahia (Hellmayr 1906). However, he later changed his opinion, deeming *T. auricapilla* invalid given its non-diagnosability across a wider latitudinal cline (Hellmayr 1936).

The eastern population of *Trichothraupis* was known for several years (1802–1850), but ornithologists only acknowledged the existence of the western population much later (e.g. Taczanowski 1874). However, little consideration has been given to possible differences between the Atlantic and Andean populations. Hellmayr (1936) noted that Andean birds have "very slightly paler" underparts, but considered the divergence "too insignificant to justify recognition in nomenclature". Zimmer remarked that "there is a slight possibility that distinctions might be found in Peruvian specimens as compared with Paraguayan and Brazilian material, but the range of variation in the species is so great (...) that little is to be expected" (Zimmer 1947). Nevertheless, Hilty (2011) suggested that further investigation is needed to determine whether two allopatric taxa are involved. Despite the suggestions of earlier authors, no taxonomic review has been conducted for this species.

A recent study demonstrated that the Atlantic and Andean populations of *T. melanops* are genetically isolated, and therefore, that the current classification as a monotypic species should be revisited (Trujillo-Arias *et al.* 2018). The Atlantic and Andean populations of the species are differentiated in the mitochondrial genome ($F_{st}=0.82$), showing each region's unique haplogroups. The estimated divergence time between regions suggests the mid-Pleistocene, and coalescent gene flow estimates indicated that both populations are isolated (i.e., migration between populations $M<1$ individual per generation). Thus, an analysis of the phenotypic variation of *T. melanops* was deemed necessary to determine the taxonomic status of the populations (Trujillo-Arias *et al.* 2018).

The authors were familiar with Atlantic *T. melanops* from field observations and study skins, but, when visiting American and European museums of natural history in 2012, we by chance opened the *T. melanops* trays with series from both the Andean and Atlantic populations, in which the plumage differences were immediately evident. The fact that the Atlantic and Andean populations of *T. melanops* have been never treated as different taxa is intriguing. Other morphologically distinct avian species that are allopatrically distributed over the south-central Atlantic Forest and in Andean slopes, and that used to be considered subspecies (e.g. *Penelope obscura/bridgesi*, *Elaenia sordida/obscura*, *Laniisoma elegans/buckleyi*, *Turdus subalaris/nigriceps*) are currently recognized as taxonomically distinct at the species level (Billerman *et al.* 2022).

In this paper, we evaluate the morphology, plumage, and vocalizations of the Atlantic and Andean populations of *Trichothraupis melanops*, discuss these results considering the genetic divergence between populations, and describe the unnamed Andean population as a new species.

Methods

We examined the plumage and morphological characters of 581 skin specimens of *Trichothraupis* housed in the following institutions: American Museum of Natural History (AMNH), New York, USA; Carnegie Museum of Natural History (CMNH), Pittsburgh, USA; Louisiana State University Museum of Natural Science (LSUMZ), Baton Rouge, USA; Museo Argentino de Ciencias Naturales “Bernadino Rivadavia” (MACN), Buenos Aires, Argentina; Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, Brazil; Muséum National d’Histoire Naturelle (MNHN), Paris, France; and The Natural History Museum (BMNH), Tring, UK. The bills, tarsi, wings, and tails of 366 specimens of *T. melanops* were measured. Some 314 came from the Atlantic, and 52 from the Andean population. A list of examined specimens is given in Appendix 1. Details of the genetic analysis were presented elsewhere (Trujillo-Arias *et al.* 2018).

Plumage was studied through qualitative comparisons aimed at testing the divergence between the Atlantic and Andean populations. A color catalog (Smithe 1975) was used to classify plumage coloration. Exposed culmen, bill height and width, tail, tarsus length, and wing chord were measured following standard procedures (Eck *et al.* 2011). Multifactorial Multivariate Analysis of Variance (MANOVA) was used to compare trait values among sexes and populations (Atlantic and Andean), and Principal Component Analysis (PCA) was conducted to summarize the correlations among the morphological variables, using R software, v. 3.3.1 (R Core Team 2022).

To investigate possible geographic variations in vocalizations, qualitative characters in both call and loudsong available in online repositories (xeno-canto.org, wikiaves.com.br, and the Macaulay Library) were considered. At the time of writing, there were 539 recordings of *Trichothraupis melanops* available in online collections. Most were for the Atlantic population (355 in WikiAves, 76 in Xeno-Canto and 89 in Macaulay Library). Only 3% were for the Andean population (eight in Xeno-Canto and 11 in Macaulay Library). Spectrograms were produced with the warbleR package (Araya-Salas & Smith-Vidaurre 2017).

Results

Plumage analysis. In both Andean and Atlantic adult male specimens, the lesser, median, and greater upper wing coverts, as well as the remiges, are all a very dark gray, similar to the tail. A speculum is formed by white patches on the inner webs, at about a third of their length, of primary remiges 2–7 or 8 and secondary remiges 2–6. The underwing coverts are also white. The underparts are mostly cream-colored and become a more buff-yellow in the undertail coverts, and in the indistinct pectoral band (Fig. 1). Label data point to the bill and tarsi being dark gray to black, and the iris being dark brown. Adult males of the Andean population, however, have grayish-olive upperparts, which become slightly paler and yellower in the rump and upper tail coverts (Fig. 1), as opposed to more uniformly olive upperparts in Atlantic populations. The crown has a bright orange-yellow crest; and only in some Andean specimens (LSUMZ 171459, 90993) is the crest variably bordered by black in the nape. The tail of Andean birds is a very dark gray (darker than blackish-neutral gray in Atlantic populations). The forehead, lores, and periorbital area in Andean and Atlantic populations are all black, forming goggles. However, males of Andean birds have completely black auriculars, although in a few male specimens (LSUMZ 96899, 169147) these become grayish-olive posteriorly. Black, however, is never as restricted in Andean specimens as in the Atlantic population of *T. melanops*.

Females of both Atlantic and Andean populations differ from males in that they lack black goggles and yellow crests. The forehead and sides of the face are instead closer to a brownish olive, and the top of the head is greenish, with a very faint variable yellowish tinge. Rectrices and remiges are dusker than in males, tending towards a dusky brown, and thus contrast less with the back. The underparts are generally darker than in males, varying between a clay color and cinnamon, but lighter and less orange among Andean populations, with uniform underparts; Atlantic population females show a subtly, but consistently, darker shade of the breast (Fig. 2). Juvenile males are like females, but most already show a yellow crest, smaller than in adults, and mixed with green.

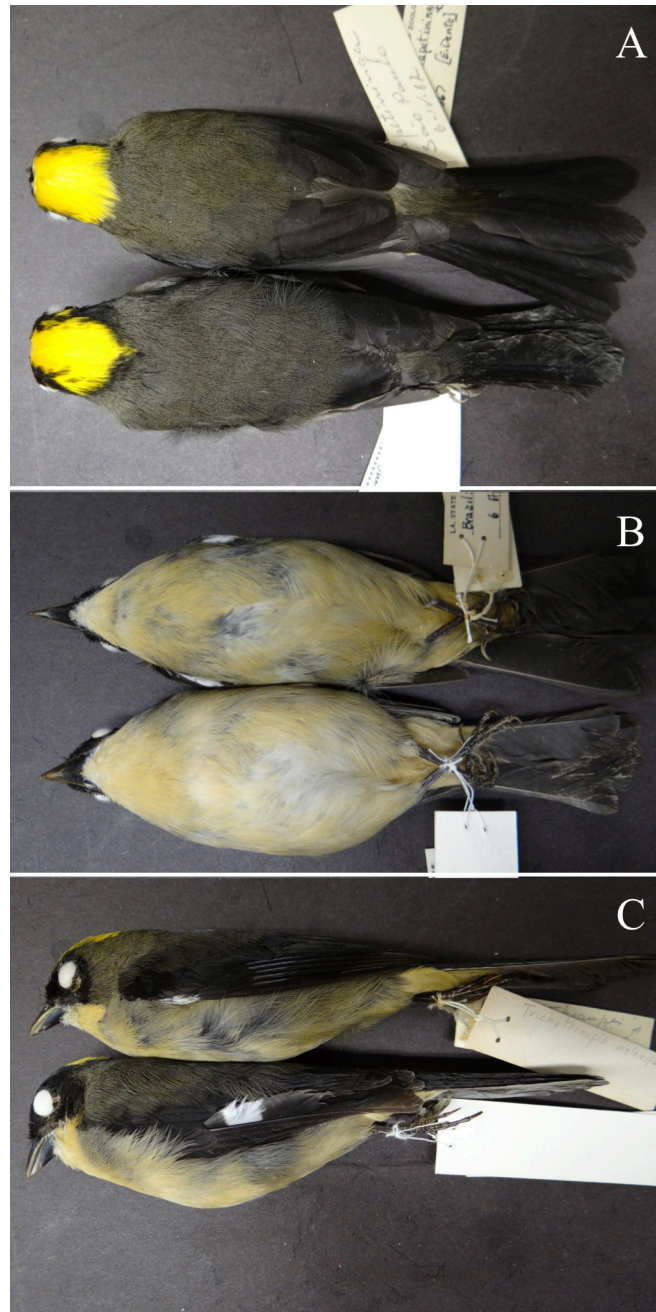


FIGURE 1. Dorsal (a), ventral (b), and lateral (c) views of males of the Atlantic (LSUMZ 53115, Itapetininga, Brazil; above) and Andean (LSUMZ 171459, Samipata, Bolivia; below) populations of *Trichothraupis melanops*.

Morphometrics. The Andean population has significantly shorter tarsi, on average, than the Atlantic population, but all traits show measurement overlap. The mean measurements of both populations are shown in Table 1. Principal Component Analysis indicates that morphometrics segregate the two populations, although incompletely (Fig. 3). Within this context, the two-factor comparison of sex and populations only showed significant differences for culmen ($p < 0.010$) and wing ($p = 0.000$) measurements between sexes, while tarsi measurements ($p = 0.000$) were significantly shorter among Andean populations (Table 1). There were no significant differences in the interactions between them (Bonferroni post hoc test $p > 0.02$). Therefore, the Andean population is morphologically distinguished based on plumage color patterns and tarsus length (Table 2).

Vocalizations. Of the recordings of the Andean population, only two were loudsongs, and only one consisted of a reasonable-quality recording to allow for the creation of spectrograms. The lack of Andean data precluded us

from quantitatively analyzing loudsongs. Qualitative inspections failed to find visual differences between contact calls (Fig. S1). The Atlantic loudsong is clearly composed of a series of upslurred and downslurred notes, forming a “W” shape. It seems to share a two-note homologous pattern with the Andean loudsong, but the number of loudsong emissions within the recording did not allow for further evaluation (Fig. S2).

TABLE 1. Descriptive statistics (mean, standard deviation [SD], sample size [N], and minimum and maximum range) of the morphometrics of *Trichothraupis melanops*.

Measurements	Males				Females			
	Andean		Atlantic		Andean		Atlantic	
	mean ± SD (N)	range	mean ± SD (N)	range	mean ± SD (N)	range	mean ± SD (N)	range
Exposed culmen	9.86 ± 1.83 (12)	8.98–14.95	9.20 ± 0.86 (157)	8.65–12.78	9.69 ± 0.91 (13)	10.51–13.93	9.38 ± 0.81 (113)	9.22–13.09
Bill height	5.92 ± 0.32 (11)	5.38–6.56	5.81 ± 0.28 (112)	5.04–6.38	6.19 ± 0.34 (11)	5.61–6.72	6.00 ± 0.28 (77)	5.23–7.43
Bill width	7.10 ± 0.81 (13)	6.04–8.59	7.72 ± 0.52 (156)	6.16–9.44	6.94 ± 0.65 (12)	6.06–8.3	7.75 ± 0.52 (112)	6.35–8.81
Tarsus length	19.62 ± 0.76 (30)	17.63–21.38	20.53 ± 0.73 (157)	19.0–22.45	19.40 ± 0.98 (23)	17.15–22.41	20.51 ± 0.78 (115)	19.0–21.95
Wing chord	80.80 ± 3.15 (31)	74.0–89.0	78.49 ± 3.11 (161)	71.0–85.0	78.13 ± 3.14 (23)	72.5–85.0	76.85 ± 3.14 (115)	70.5–82.0
Tail length	73.46 ± 2.73 (31)	68.0–79.0	74.92 ± 2.69 (153)	68.0–82.5	73.08 ± 2.77 (24)	67.0–79.0	74.40 ± 2.75 (112)	68.0–80.5
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Bill height	5.92 ± 0.32 (11)	5.38–6.56	5.81 ± 0.28 (112)	5.04–6.38	6.19 ± 0.34 (11)	5.61–6.72	6.00 ± 0.28 (77)	5.23–7.43
Bill width	7.10 ± 0.81 (13)	6.04–8.59	7.72 ± 0.52 (156)	6.16–9.44	6.94 ± 0.65 (12)	6.06–8.3	7.75 ± 0.52 (112)	6.35–8.81
Tarsus length	19.62 ± 0.76 (30)	17.63–21.38	20.53 ± 0.73 (157)	19.0–22.45	19.40 ± 0.98 (23)	17.15–22.41	20.51 ± 0.78 (115)	19.0–21.95
Wing chord	80.80 ± 3.15 (31)	74.0–89.0	78.49 ± 3.11 (161)	71.0–85.0	78.13 ± 3.14 (23)	72.5–85.0	76.85 ± 3.14 (115)	70.5–82.0
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TABLE 2. Results from a Multifactorial Multivariate Analysis of Variance between the Atlantic and Andean populations of *Trichothraupis melanops*.

	Population	Interaction	Residuals
Culmen	1.99	0.48	210.12
Tarsus	44.79	0.07	128.57
Wing	7.68	18.23	2303.49
Tail	25.63	7.59	1968.47
Degrees of freedom	1	1	281



FIGURE 2. Dorsal (a) and ventral (b) views of females of the Atlantic (LSUMZ 53117, Salesópolis, Brazil; above) and Andean (LSUMZ 90992, Serranía Bellavista, Bolivia; below) populations of *Trichothraupis melanops*.

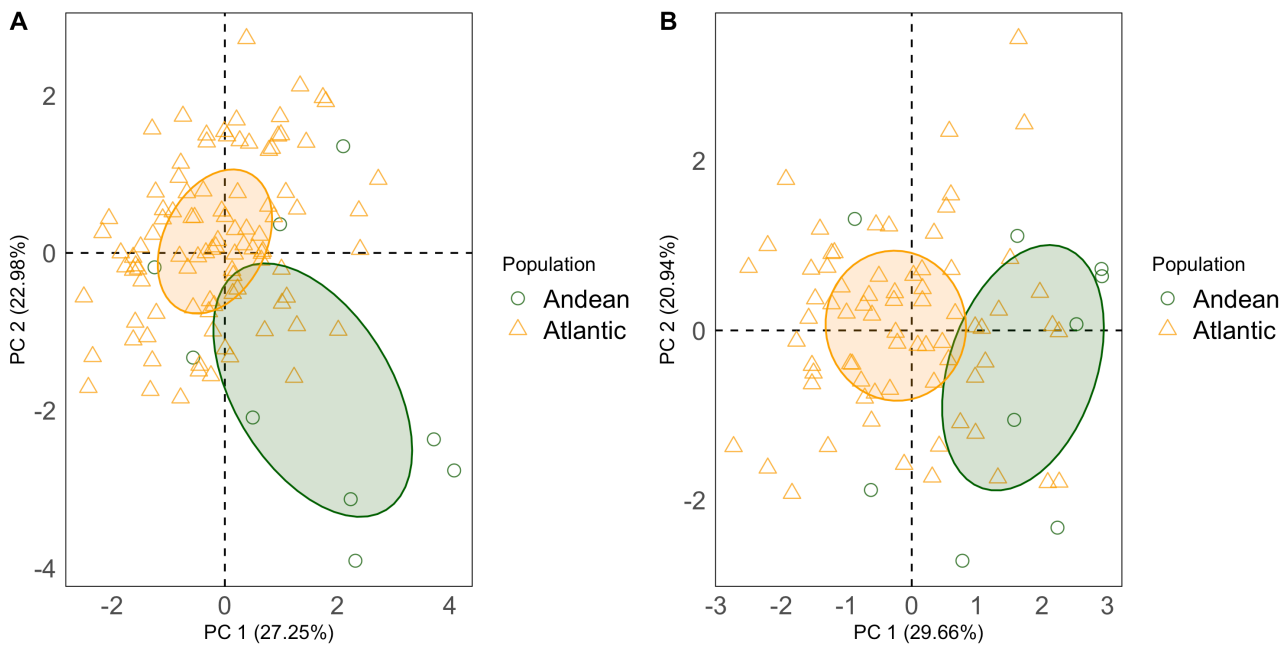


FIGURE 3. Principal Component Analysis of Atlantic Forest (orange) and Andean (green) populations of *Trichothraupis melanops*. No morphometric segregation was found for males (A) or females (B).

Nomenclature. The question then arises as to which population the name *T. melanops* applies. There are no type specimens, but the type locality is inferred to be southern Paraguay, where Don Pedro Blas Noséda lived, and upon whose report Azara (1802) described the species. Additionally, Noséda (Azara 1802) described the bird's back as being brown (“*El costado de la cabeza y el occipucio hasta la cola pardos.*”), which is a diagnostic character of the Atlantic Forest population in relation to the Andean population (Fig. 1, Fig. S3). Thus, the name *T. melanops* is undoubtedly applicable to the Atlantic population. No available name, to the best of our knowledge, applies to the Andean population, which we hereby describe as a new species under the Phylogenetic Species Concept. In addition, body adornments commonly assumed to be important for sexual selection in males (crown, throat, and breast coloration) differ between *Trichothraupis* populations. These observations are as evident as in other closely related pairs of species with the same distribution pattern which are undoubtedly separate species, such as *Amazona pretrei/tucumana* and *Arremon flavirostris/dorbignii*. Despite being allopatric, they have been split according to several criteria, such as minor color differences, song divergence and genetic isolation (Trujillo-Arias *et al.* 2017). These taxa experience only low gene flow and have temporally diverged around the same time as did Andean and Atlantic *Trichothraupis* (0.6–0.8 million years ago), and thus we consider that specific status is warranted for the Andean population of *Trichothraupis* under the Biological Species Concept as well, which we thus describe in the following.

***Trichothraupis griseonota* sp. nov.**

Proposed vernacular names: Andean Black-goggled Tanager (English); tiê-de-topete-andino (Portuguese); Frutero corona amarilla andino (Spanish).

Holotype. MACN 8979a, Male. BOLIVIA, Buenavista, Santa Cruz, 30 July 1916, J. Steinbach *leg.*, 450 m.

Paratypes. MACN 72807, Male. BOLIVIA, Pederal, Chuquisaca, Tomina, 08 October 2011, G. S. Cabanne *leg.*, 1450 m asl. Habitat type: Tucumano-Boliviano Forest. Mist-netted by GSC. Iris: brown, bill black, mandible light gray, feet gray. Tissue sample MACNCTOR 6286. Weight: 21.75 g, skull ossification 100 %, bursa 3x3 mm, testis 4x3 mm. MACN 8979b, Female. BOLIVIA, Buenavista, Santa Cruz, 30 July 1916, J. Steinbach *leg.*, 450 m.

Etymology. From Latin *griseo* (gray) and *nota* (mark), highlighting one of the most distinctive plumage characters of the new species.



FIGURE 4. *Trichothraupis melanops* (above) and *T. griseonota* **sp. nov.** (below). Plate by Eduardo Brettas.

Diagnosis. Four fixed plumage traits and one morphometric trait diagnose *Trichothraupis griseonota* from its sister species, *T. melanops*. The first and most noteworthy is the black facial mask. In the new species, it includes the auricular region (Fig. 1; Fig. S3), whereas in *T. melanops* this mask is only a narrow line behind the eye, not reaching the auriculars. In a few Atlantic specimens (AMNH 774505, LSUMZ 59405, MZUSP 27851) there is some black in the auriculars, but in those cases, it is mixed with green, producing a mottled appearance, unlike the homogeneous black in *T. griseonota*. A second diagnostic character is the paler underparts of adult males and females. This is especially evident in the undertail coverts, which are a cream color to buff-yellow in *T. griseonota*, versus cinnamon in *T. melanops*, and in the chest, in which both species have a more orange tone than in the belly, but less distinctly so in the new species, where the color of the chest is more buff-yellow, versus buff in *T. melanops* (Fig. 1). Adult females of *T. griseonota* are also somewhat paler in the underparts than in *T. melanops*, but the difference is not as pronounced as in males, and sexual dimorphism of plumage color in the underparts is more evident in *T. griseonota* than in *T. melanops*. The third plumage characteristic is the color of the back of adult males, which is greyer in *T. griseonota*, versus being more greenish-olive in *T. melanops* (Fig. 1; Fig. S3). The last character in which the two species differ is the breast coloration of females, which is subtly but consistently darker in Atlantic populations (Fig. 2). *Trichothraupis griseonota* also has significantly shorter tarsi compared to *T. melanops* (Fig. 4).

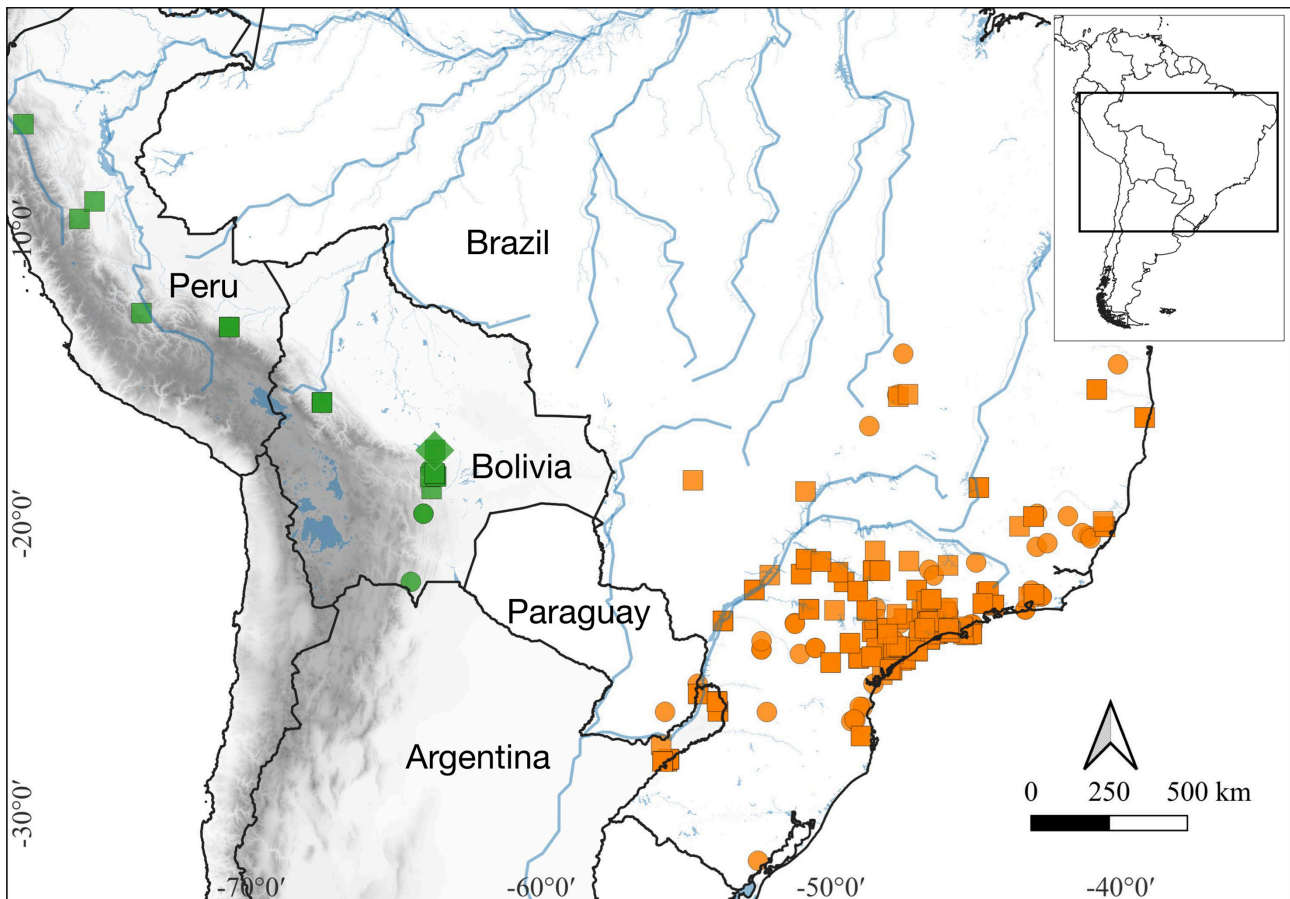


FIGURE 5. Distribution of *Trichothraupis melanops* (orange) and *T. griseonota* sp. nov. (green) in South America. Squares represent museum specimens and circles are recordings. A diamond indicates the type locality of *T. griseonota*; there is no type locality for *T. melanops*. South America is represented in the inset.

Description of holotype. The front, loreal, superciliary, and auricular regions are black; the nape is also black, slightly streaked above. The throat, chest, belly, and undertail coverts are pale brown, light olive-brown in the lateral chest. The crown to the nape is yellow. The back is dark olive grey (M5Y-3/2). The upper wing coverts, remiges, and rectrices are dark brown, with white underwing coverts. The base of primaries 2–7 shows a white middle band occupying the inner web of the feather, while the two outer primary feathers do not have white bands. The white band also occurs on the secondary feathers. The maxilla is greenish-black, while the mandible is black at the base. The feet are olive-brown. Total length: 161 mm. Bill length: 12.24 mm, 8.99 mm from nares to the tip; bill width 4.40 mm, height 5.34 mm. Wing chord (unflattened): 83.2 mm; tarsus length: 17.25, and tail 78.55 mm.

Description of the female paratype. The forehead, nape, loreal, crown, superciliary, and auricular region are olive. The throat, breast, and belly are pale brown. The lateral breast is light olive brown, and the undertail coverts are like the lateral breast. The back is grayish-olive, while the upper wing coverts, flight feathers, and tail are dark brown, and underwing coverts are white. The bases of the primaries (2–7) and the secondaries have a white middle band on the inner web of the feather, lacking in the two outer primary feathers. The feet are olive brown. Total length: 168 mm. Bill length: 11.76 mm. Bill length from nares to the tip: 9.00 mm, bill width 5.06 mm, bill height 5.75 mm. Wing chord (unflattened): 79.56 mm, tarsus 17.90 mm, and tail length 79.84 mm. The bill is greenish-black, and the mandible is black at the base, with a light brownish-gray tip.

Distribution. *Trichothraupis griseonota* is restricted to the eastern slope of the Andes of central and southern Peru, Bolivia, and northwestern Argentina (Fig. 5). It inhabits the Seasonal Dry Tucumano-Boliviano Forests which are confined to the northwestern Argentinean Andean forests and foothills north to central and southern Bolivia. The species also occurs along a narrow strip of Yungas Forests in northern Bolivia and Peru, at the base of the Andes. These montane forests exhibit higher moisture levels compared to the Tucumano-Boliviano Forests.

Discussion

Our study of plumage revealed full diagnosability between the Atlantic and Andean populations of *Trichothraupis*. Both populations are also differentiated by tarsus length, with the Atlantic population having longer tarsi on average. Additionally, the taxa inhabit distinct vegetation types (Atlantic Forest versus Tucumano-Boliviano and Yungas montane forests). These results are in full agreement with a previous study, which indicated that these populations are divergent and genetically isolated (Trujillo-Arias *et al.* 2018). Atlantic and Andean populations show levels of gene flow insufficient to preclude their evolutionary divergence (i.e., migration between populations $M < 1$ individual per generation) (Trujillo-Arias *et al.* 2018). Therefore, the current classification of *Trichothraupis* as a monotypic species has proven inadequate to reflect its evolutionary history.

Molecular studies have shown that *Trichothraupis* is part of a distinct clade that also includes most species of *Tachyphonus* and all the species in *Lanio*, *Coryphospingus*, *Rhodospingus*, and *Eucometis*, the latter genus being a sister-group to *Trichothraupis* (Burns *et al.* 2014). The recently described *Heliothraupis oneilli* Lane *et al.*, 2021 from the foothills of the Andes in Peru and Bolivia proved to be most closely related to *Trichothraupis*, which was then considered monotypic (Lane *et al.* 2021). This further evidence is yet to be considered in the complex biogeographic history that brings together Atlantic Forest and Andean birds (Cabanne *et al.* 2019).

Few sound recordings are available for the Andean populations, but it has been suggested that *Trichothraupis* individuals from the Andes are not as vocal as those from the Atlantic Forest (Lane *et al.* 2021). Contact calls are visually identical in spectrograms and sound quite similar for both allopatric populations, but for most passerines, when sister clades are morphologically and genetically distinct, supposedly homologous loudsongs also typically differ quantitatively, including for Neotropical oscine and suboscine species (Isler *et al.* 1998; Bocalini & Silveira 2016). Therefore, we also recommend analyzing more loudsongs as more recordings of *T. griseonota* are made available.

The fact that these distinct lineages had not been recognized before is somewhat intriguing, given that *Trichothraupis* is a common species, abundantly represented in collections, which has been known to ornithological science since at least the early 19th century. The taxon was suggested to be the objective of future species limits investigation in a paper whose primary aim was not taxonomic (Trujillo-Arias *et al.* 2018). What is even more remarkable is that our initial 10-year-old insight that there might be two species came not from an encounter with an unfamiliar bird during fieldwork, or vocal analysis, as has been the case with most new bird species described in the last several years (Fjeldså 2013), but instead from the oldest, most traditional form of practicing avian taxonomy: the examination of skin specimens in natural history museum collections. Many authors have lamented the declining appreciation of museum collections, traditional specimens, and the study of morphology (Winker 2004; Pyke & Ehrlich 2010; Joseph 2011; Giribet 2015). The pleas of these authors for reversing this trend have been largely based on the importance of specimens for environmental and conservation science (Winker 2004; Pyke & Ehrlich 2010) or for molecular phylogenetics, either as sources of ancient DNA (Staats *et al.* 2013) or, in the case of fossils, as calibration points (Giribet 2015). In describing a new species discovered in museum cabinets, we highlight that, in addition to extremely important and relatively new paradigms, museum specimens are especially important in the age of genomes and supercomputers, given that their most important role since their inception centuries ago has been to serve as the cornerstone upon which avian taxonomy is based. By documenting and organizing variations and allowing for insights such as this, we hope that the discovery of *T. griseonota* will serve as a reminder for ornithologists never to underestimate the possibility that exciting new discoveries may lie among a seemingly mundane series of bird skin specimens.

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Supplementary Materials. The following supporting information can be downloaded at the DOI landing page of this paper:

FIGURE S1. Spectrograms of contact calls of the (A) Atlantic (WA4980414, Marechal Floriano, Espírito Santo) and the (B) Andean (XC4090, Chuquisaca, Bolivia) populations of *Trichothraupis melanops*.

FIGURE S2. Spectrograms of loudsongs of the (A) Atlantic (ML201641, Misiones, Argentina) and the (B) Andean (XC35966, Santa Cruz, Bolivia) populations of *Trichothraupis*. Dashed lines indicate a “W” shape of the loudsong, while a rectangle indicates possible homologous notes.

FIGURE S3. Males of (A) *Trichothraupis melanops* (Santo Antônio do Pinhal, São Paulo, Brazil) and (B) *T. griseonota* **sp. nov.** (Masicuri, Santa Cruz, Bolivia). Photos by Alexandre Gualhanone and Jacob Wijpkema.

APPENDIX 1. Specimens examined.

Trichothraupis melanops.—ARGENTINA: 25km S-SE of Colonia Garabi: 1♂ AMNH 799105; Arroyo Uruguai, km 10: 36♂ AMNH 774483, 774484, 774485, 774486, 774487, 774488, 774490, 774491, 774493, 774495, 774496, 774497, 774498, 774499, 774500, 774501, 774502, 774503, 774504, 774505, 774506, 774507, 774508, 774510, 774511, 774513, 774518, 774519, 774521, 774523, 774524, LSUMZ 36921, 59383, 59387, 59388, 59389, 8♀ AMNH 774528, 774529, 774530, 774531, 774532, 774534, 2♀ LSUMZ 36922, 59385; Arroyo Uruguai, km 15: 1♂ LSUMZ 59393; Arroyo Uruguai, km 30: 17♂ AMNH 774509, 774512, 774515, 774516, 774517, 774520, LSUMZ 59394, 59395, 59397, 59398, 59399, 59402, 59405, 59408, 59410, 59411, 59414, 9♀ AMNH 774525, 774526, 774527, 798139, 59413, LSUMZ 59396, 59400, 59406, 59407; Barra Concepcion: 16♂ AMNH 798142, 798143, 798144, 798145, 798146, 798147, 798191, LSUMZ 59366, 59370, 59371, 59372, 59373, 59374, 59375, 59376, 59378, 4♀ AMNH 798148, LSUMZ 59369, 59377, 59379; Cnia Garabí, Ea. Rincón de las Mercedes: 10♂ LSUMZ 59418, 59421, 59422, 59423, 59425, 59426, 59428, 59431, 59432, 59433, 7♀ LSUMZ 59415, 59419, 59420, 59424, 59427, 59429, 59430; Col. Garabí, Ea. Rincon de Las Mercedes: 10♂ AMNH 798150, 798151, 798152, 798153, 798154, 798155, 798156, 798157, 798158, 798159, 8♀ AMNH 798149, 798160, 798161, 798162, 798163, 798164, 798165, 798166; Garruchos: 7♂ AMNH 780662, 780664, 780665, 780666, 780667, CMNH 141029, 141163, 3♀ AMNH 780663, 780668, CMNH 141030; Parada Reis, Ea. Chantecler: 1♂ AMNH 798167, 1♀ LSUMZ 59380; Posadas: 1♂ AMNH 511045; Puerto Bosetti: 1♂ CMNH 141179, 1♀ LSUMZ 59382; San Javier 1♂ AMNH 511046; San José 1♀ AMNH 798140. BRAZIL: 11♂ AMNH 40923, 140162, 511057, 511058, 511059, 511060, 511061, 511062, MNHN 1933n612, 1933n613, MZUSP 8992, 1♀ MZUSP 8991; Rio Grande, E. F. S. J.: 1♂ MZUSP 51215; Bahia: Jaguaquara: 1♂ AMNH 245569; Espírito Santo: Chaves (Santa Leopoldina): 2♂ MZUSP 28371, 28372, 1♀ MZUSP 28370; Santa Tereza: 1♂ MZUSP 28373; Serra do Caparaó, Segredo do Veado: 3♂ AMNH 318051, 318052, 318053, 3♀ AMNH 318054, 318055, 318056; Victoria: 2♂ AMNH 511052, 511053; Goiás: Fazenda Transvaal: 1♂ MZUSP 27851; Planaltina: 1♀ MZUSP 52031; Silvânia: 2♀ MZUSP 12434, 17470; Mato Grosso do Sul: Rio Amambahy: 1♀ AMNH 319621; Minas Gerais: S. José da Lagoa (Faz. Boa Esperança): 5♀ MZUSP 25856, 25858, 25859, 25860, 25861, 25862; Santa Barbara do Caparaó: 1♂ AMNH 318050; Serra do Caparaó, Fazendinha: 1♀ AMNH 317160; Serra do Caparaó, Rio Caparaó: 3♂ AMNH 317153, 317154, 317156, 1♀ AMNH 317158; Paraná: Castro: 1♂ MZUSP 6899, 1♀ MZUSP 8752; Foz do Iguaçu: 3♂ AMNH 319304, 319305, 319306, 1♀ AMNH 319307, Guaraqueçaba: 1♂ MZUSP 91300; Guaíra: 3♂ AMNH 319294, 319295, 319296, 3♀ AMNH 319297, 319298, 319299; Porto Camargo, Rio Paraná: 5♂ MZUSP 37119, 37120, 37121, 37122, 37123; Porto Mendes, Rio Paraná: 1♂ AMNH 319303; Tibagy (Fazenda Monte Alegre): 1♂ AMNH 319289; Rio de Janeiro: Maromba, Parque Nacional do Itatiaia: 1♂ MZUSP 34896; Monte Serrat, Serra do Itatiaia: 1♂ AMNH 189384; Neu Freiburg: 1♀ AMNH 511056; Ponte Maromba, Serra do Itatiaia: 2♀ AMNH 189385, 189386; Ribeirão Maromba, Mauá: 1♂ MZUSP 36484, 1♀ MZUSP 36483; Teresópolis (C. Guinle): 1♂ MZUSP 33833, 1♀ MZUSP 33832; Therezópolis, Organs Mts.: 4♂ AMNH 147207, 147208, 147210, 147212, 2♀ AMNH 147209, 147211; Rio Grande do Sul: K 232, BR-285, Carazinho: 1♀ AMNH 810540; Morro Pelado, Canela: 1♀ AMNH 813090; Parque Nacional do Itatiaia: 3♂ MZUSP 36187, 36188, 36189; Petrópolis: 2♂ AMNH 511047, 33831; Santa Catarina: Nova Trento: 1♂ MZUSP 91304; Palmital (São Francisco): 1♂ AMNH 316454; Salto Pirahy (Joinville): 8♂ AMNH 316443, 316445, 316446, 316447, 316448, 316449, 316450, 316451, 2♀ AMNH 316452, 316453; São Paulo: Alambary: 3♂ AMNH 511054, 511055, 511055; Alto da Serra, Paranapiacaba: 1♂ MZUSP 4840, 4♀ MZUSP 4815, 6507, 4761, 79916; Barra do Icapara: 2♀ MZUSP 63178, 69741; Barra do Rib. Onça Parda: 2♂ MZUSP 57826, 57827, 3♀ MZUSP 57823, 57824, 57825; Barra do Rio Guaraú: 1♀ MZUSP 51749; Barreiro Rico, Anhembi: 10♂ MZUSP 54712, 54713, 54714, 54719, 54720, 54721, 54722, 54723, 54724, 54725, 7♀ MZUSP 54711, 54715, 54716, 54717, 54726, 54727, 54728; Bauru, Rio Feio: 1♂ MZUSP 1987; Bebedouro: 1♂ MZUSP 4565; Boracéia: 3♀ MZUSP 28041, 31733, 33982; BR-2, km 76: 1♀ MZUSP 54365; Buri: 2♂ MZUSP 75607, 76712, 1♀ MZUSP 75608; Cach. Das Flores, Rio Paranapanema, distrito de Assis: 2♂ MZUSP 29408, 29410; Campanario São Francisco Ranch: 2♂ AMNH 319623, 319624; Can Can, rio Feio: 1♂ MZUSP 5801, 1♀ MZUSP 5719; Cananéia, Tabatinguera 1♂ MZUSP 15542;

Caraguatatuba: 1♂ MZUSP 78709; Casa Grande, Salesópolis 14♂ MZUSP 61181, 61182, 61247, 62787, 62788, 62789, 62790, 62792, 62793, 64564, 64593, 64660, 64664, 64665, 4♀ MZUSP 62786, 64594, 64662, 64663; Cor. Das Flores, distrito de Assis, Rio Paranapanema: 1♂ MZUSP 29409; Costão dos Engenhos: 1♂ MZUSP 72712; Coxim: 1♀ MZUSP 17283; Eldorado Paulista: 1♂ MZUSP 54366; Engenheiro Reeve: 1♂ AMNH 511048; Estação Biológica de Boracéia, Salesópolis: 11♂ MZUSP 52104, 70605, 70629, 70630, 70631, 70632, 78497, 80302, 92239, 92242, 93255, 3♀ MZUSP 78498, 92241, 93254; Estação Ecológica de Bananal: 6♂ MZUSP 78415, 78416, 78417, 93557, 93559, 1♀ 93558; Estação Engenheiro Ferraz: 6♂ MZUSP 55656, 57817, 57821, 57822, 60993, 60994, 5♀ MZUSP 55657, 57818, 57819, 57820, 60995; Estação Vera Cruz, Porto Seguro: 2♂ MZUSP 76245, 76246; Estrada Interna (poste 26), Ilha do Cardoso, Cananéia: 1♀ MZUSP 70686; Estrada Petrobrás, km 38.7, Caraguatatuba: 1♂ MZUSP 66143; Faz. Duas Barras, Santa Maria do Salto: 2♂ MZUSP 94475, 94476, 3♀ MZUSP 94477, 94478, 94479; Faz. Intervalos: 1♀ MZUSP 66119; Fazenda Montes Claros, São José dos Campos: 2♂ MZUSP 91702, 91703; Fazenda Barreiro Rico, Anhembi: 2♂ MZUSP 42855, 43372, 1♀ MZUSP 43301; Fazenda Boa Esperança, Ribeirão do Largo: 1♂ MZUSP 80460, 1♀ MZUSP 80461; Fazenda Bom Jesus, Monte Alegre: 2♂ MZUSP 29064, 28775; Fazenda Cambuhy, Matão: 3♂ MZUSP 81687, 81690, 81691, 2♀ MZUSP 81688, 81689; Fazenda Jacaré-Riachão, Felixlândia: 3♀ MZUSP 79189, 79197, 79198; Fazenda Palmira, Rio Paranapanema: 1♂ MZUSP 29407; Fazenda Pedras, Avaré: 2♂ MZUSP 54050, 54054, 3♀ MZUSP 54056, 54057, 54058; Fazenda S. Miguel, Cajuru: 1♂ MZUSP 29121; Fazenda Sant'Ana (Matão) m. de Serra Negra: 1♂ MZUSP 31343; Fazenda Santa Isabel, Ibiti: 1♂ MZUSP 31340; Fazenda Santa Maria, Lucélia: 1♂ MZUSP 31770, 1♀ MZUSP 31771; Floresta Estadual Itapetininga, Itapetininga: 5♂ MZUSP 62779, 62782, 62783, 62784, 62785, 2♀ MZUSP 62780, 62781; Hansa: 1♂ AMNH 316455; Icapara: 1♂ MZUSP 72710; Iguape: 1♂ MZUSP 67584; Ilha de São Sebastião: 1♀ MZUSP 5942; Ilha dos Búzios: 3♂ MZUSP 63699, 63700, 63701, 2♀ MZUSP 63698, 63829, 50888; Iporanga: 1♀ MZUSP 31112; Itacaré: 1♂ MZUSP 11827; Itapetininga: 2♂ LSUMZ 53115, 68292; Itararé: 1♂ MZUSP 11801, 2♀ AMNH 140163, MZUSP 4044; Itatiba: 1♂ MZUSP 87; Lins, Campestre: 1♂ MZUSP 28708, 1♀ MZUSP 28709; Matão: 1♂ MZUSP 88404; Onça Parda: 1♀ MZUSP 49201; Ourinho: 1♀ MZUSP 1858; Parque Estadual da Cantareira, Núcleo Pedra Grande: 2♂ MZUSP 87860, 87862; Pico do Cardoso, Ilha do Cardoso, Cananéia: 1♀ MZUSP 70685; Piquete: 1♂ AMNH 511049; Porto Cabral, Rio Paraná: 4♂ MZUSP 27529, 27530, 27531, 27532; Presidente Epitácio: 1♀ MZUSP 11324; Primeiro Morro: 1♂ MZUSP 50882, 2♀ MZUSP 50883, 50884; R. Ribeira, Embu: 1♀ MZUSP 69742; Reserva Florestal Morro Grande, Caucaia do Alto: 1♀ MZUSP 78882; Ribeirão Fundo: 1♂ MZUSP 50889, 3♀ MZUSP 50885, 50890, 50891; Rio das Pedras, Piracicaba: 2♂ MZUSP 3072, 8626; Rio Feio: 2♀ MZUSP 5612, 5613; Rio Guaraú, Barro Branco: 1♀ MZUSP 51750; Rio Ipiranga, Tamanduá: 1♂ MZUSP 49200, 1♀ 49199; Rio Juquiá, Faz. Poço Grande: 2♂ MZUSP 23774, 24055, 3♀ MZUSP 24053, 24054, 24056; Salesópolis, Casa Grande: 7♂ LSUMZ 51512, 52790, 53116, 63508, 67865, 68082, 68293, 3♀ LSUMZ 53117, 53118, 67866; Santos, rio Guaratuba: 8♂ LSUMZ 63499, 63500, 63501, 63502, 63503, 63504, 63505, 63507, 2♀ LSUMZ 63498, 63506; São Bernardo: 1♂ MZUSP 51214, 1♀ MZUSP 51213; São Bernardo do Campo, torre 728, linha Itaberá-Tijuco Preto: 1♂ MZUSP 75544, 1♀ MZUSP 75545; São Sebastião: 1♂ AMNH 511051, 2♀ AMNH 511050, MZUSP 1204; Serra da Bocaina: 1♂ MZUSP 27087, 2♀ MZUSP 27086, 27088; Serra da Cantareira: 1♂ MZUSP 15851; Serra da Cantareira, Mairiporã: 5♂ MZUSP 85341, 85342, 85345, 85346, 85346; Serra da Mantiqueira, São Francisco Xavier: 1♀ MZUSP 31138; Sítio Boa Vista, Monte Alegre, mun. de Amparo: 1♂ MZUSP 29049; Tabatinguara, Cananéia: 1♂ MZUSP 15544; Taboão da Serra: 1♀ MZUSP 60404; Taquaruçu: 1♂ MZUSP 72714, 1♀ MZUSP 72713; Terra Preta: 1♂ MZUSP 60437, 1♀ MZUSP 60439; Tietê: 1♀ MZUSP 3071; Tijuco Alto: 5♂ MZUSP 70316, 70317, 70319, 70320, 70322, 2♀ MZUSP 70318, 70321; Trilha da Cachoeira, Estação Ecológica de Bananal: 1♂ MZUSP 81143; Trilha da Pedra Vermelha, Estação Ecológica de Bananal: 3♀ MZUSP 81144, 81145, 81146; Valparaíso: 2♂ MZUSP 12460, 12536, 1♀ MZUSP 12458; Vanuire: 1♂ MZUSP 10924, 1♀ MZUSP 12123; Visc. De Soutello, mun. Socorro: 2♂ MZUSP 31341, 31342, 1♀ MZUSP 31344; PARAGUAY: 2♂ AMNH 748876, 748877, 1♀ AMNH 748878; East of Caaguazu: 3♂ AMNH 320716, 320717, 320718; East of Villa Rica, Colonia Independencia: 2♂ AMNH 320264, 320266, 4♀ AMNH 320267, 320268, 320269, 320270; Sapucay: 2♂ AMNH 511043, 511044, 1♀ AMNH 511042.

Trichothraupis griseonota sp. nov.—BOLIVIA: Buenavista: 1♂ MACN 8979a, 1♀ MACN 8979b; Chuchial, 37 km SE Samaipata: 3♂ LSUMZ 169146, 169148, 169147; Ichilo 3♂ MNHN 1959n1483; La Pajcha, 28 km S Samaipata: 1♀ LSUMZ 169145; Pedernal: 1♂ MACN 72807; Prov. Florida, 23.2 km E Samaipata, 1350m: 1♂ LSUMZ 171459, 4♀ LSUMZ 171460, 171461, 171462, 171463; Prov. Florida, 6.5 km S of Bermejo: 1♂ LSUMZ sn; Prov. Vallegrande, 14.5 km by road NW Masicuri: 1♂ LSUMZ 125321; Province Sara: 4♂ AMNH 511038, 511039, 511040, 511041, 4♀ AMNH 511034, 511035, 511036, 511037; Provincia Tchilo, Buena Vista: 2♂ LSUMZ 38320, 38321; Serrania Bellavista, 35 km by road N Caranavi: 2♀ LSUMZ 90994, 90996; Serrania Bellavista, 37 km by road N Caranavi: 1♂ LSUMZ 90993, 1♀ 90992; Serrania Bellavista, 47 km by road N Caranavi: 7♂ LSUMZ 90995, 96897, 96898, 96899, 96901, 96902, 96903, 3♀ LSUMZ 96900, 96904, 96905; Vermejo: 5♀ AMNH 139820, 139821, 139822, 139823, 139824; PERU: 3rd km NE Abra Divisoria on Tengo Maria - Pucallpa Hway: 1♂ LSUMZ 85505; Bosque Rio Abra, E bank of Rio Huallaga, near Chinchavito: 1♂ LSUMZ 82239; Cordillera Vilcabamba: 1♂ AMNH 820183, 1♀ 820182; Cordillera Vilcabamba, 9km E of Luisiana: 1♂ AMNH 820020; Guayabamba: 1♂ BMNH 96.10.6.199; Huanhuachayo: 1♂ LSUMZ 69578; Quincemil, Had. Cadena: 4♂ MNHN 1966n1604, 1966n1605, 1966n1606, 1966n1607, 2♀ MNHN 1966n1603, 1967n1287.

Supplementary materials

A new species of tanager (Aves, Thraupidae) from the Eastern slopes of the Andes

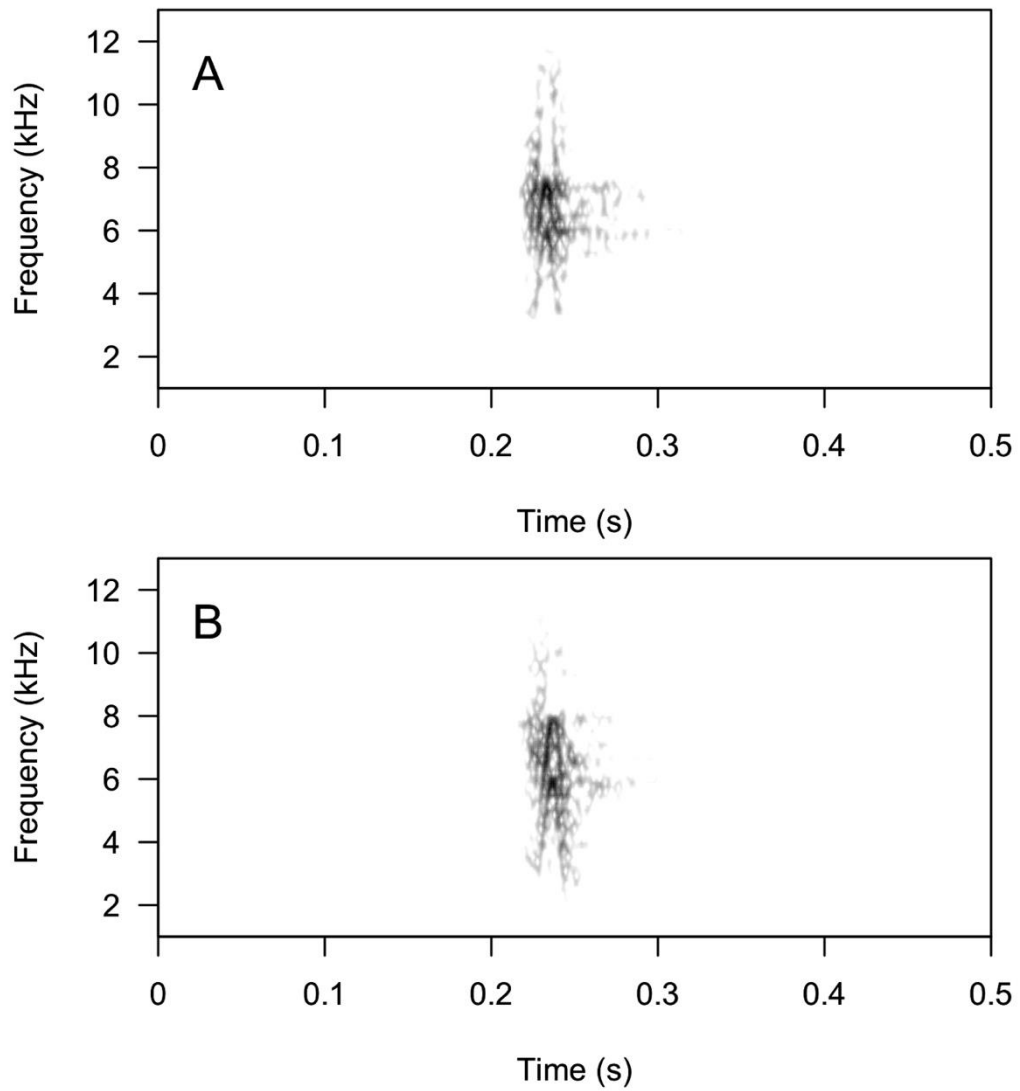


FIGURE S1. Spectrograms of contact calls of the (A) Atlantic (WA4980414, Marechal Floriano, Espírito Santo) and the (B) Andean (XC4090, Chuquisaca, Bolivia) populations of *Trichothraupis melanops*.

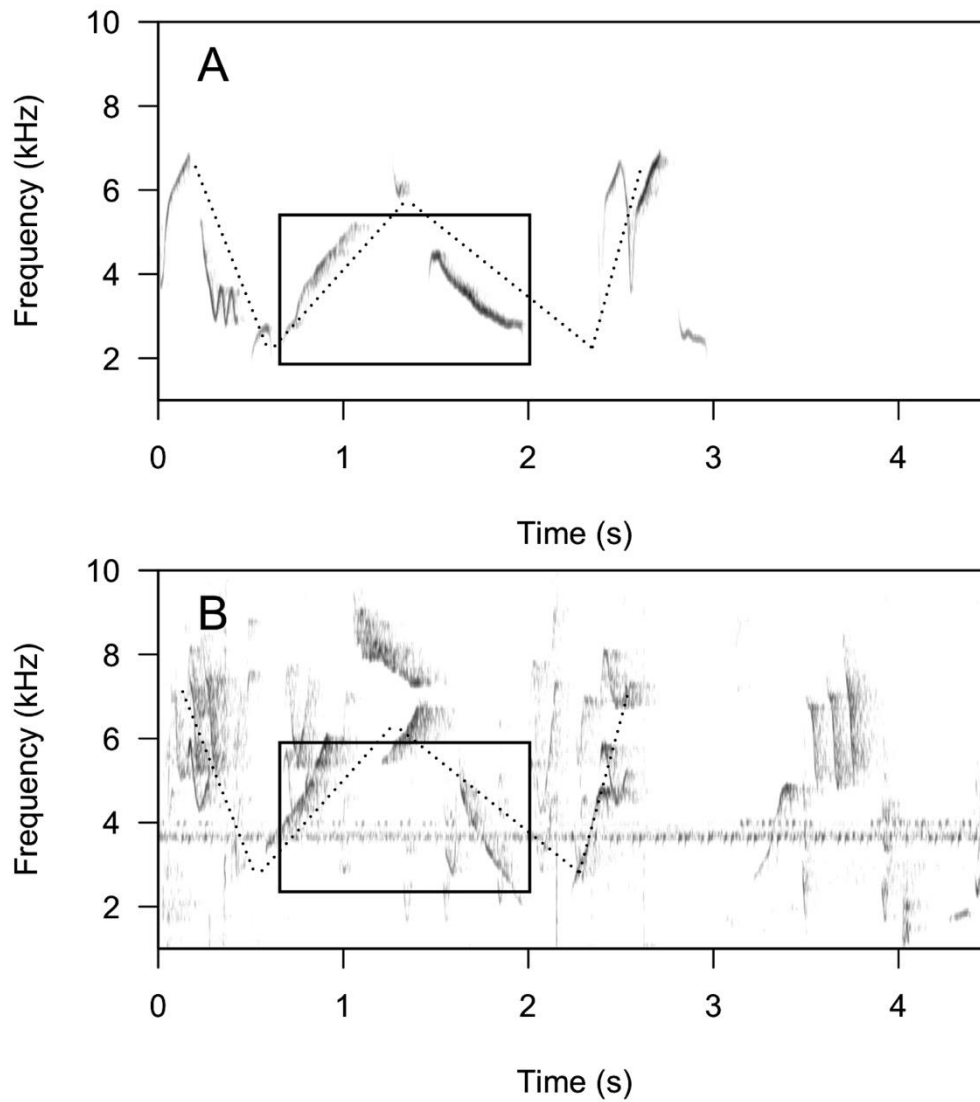


FIGURE S2. Spectrograms of loudsongs of the (A) Atlantic (ML201641, Misiones, Argentina) and the (B) Andean (XC35966, Santa Cruz, Bolivia) populations of *Trichothraupis*. Dashed lines indicate a “W” shape of the loudsong, while a rectangle indicates possible homologous notes.



FIGURE S3. Males of (A) *Trichothraupis melanops* (Santo Antônio do Pinhal, São Paulo, Brazil) and (B) *T. griseonota* **sp. nov.** (Masicuri, Santa Cruz, Bolivia). Photos by Alexandre Gualhanone and Jacob Wijpkema..