TAXONOMY OF THE GREY-AND-ORANGE TAPACULOS (AVES: PASSERIFORMES: RHINOCRYPTIDAE) OF THE NORTHERN ANDES, WITH DESCRIPTION OF A NEW SUBSPECIES OF *SCYTALOPUS GRISEICOLLIS* FROM COLOMBIA

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Trabajo de Grado presentado como requisito parcial para optar al título de Biólogo

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TITULO: TAXONOMIA DE LOS TAPACULOS *SCYTALOPUS* GRIS Y NARANJA DE LOS ANDES DEL NORTE (AVES: PASSERIFORMES: RHINOCRYPTIDAE), CON DESCRIPCION DE UNA NUEVA SUBESPECIE DE *SCYTALOPUS GRISEICOLLIS* DE COLOMBIA[*]

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PALABRAS CLAVES: *Scytalopus*, tapaculo, nueva subespecie, límites de especie, Colombia, taxonomía

DESCRIPCIÓN:

Se estudió la taxonomía de cuatro Tapaculos *Scytalopus* gris y naranjas de alta elevación del norte de los Andes orientales, Serranía de Perijá y Cordillera de Mérida en Colombia y Venezuela (*S. griseicollis*, *S. infasciatus*, *S. meridanus* y *S. fuscicauda*), combinando especímenes de museo, trabajo de campo y análisis de cantos. Variacion individual en plumaje dentro de *S. griseicollis* y *S. meridanus*, es substancial y ambas tienen un rango elevacional amplio. *S. infasciatus* no es distinguible de *S. griseicollis* en su voz, plumaje o biometría. Pieles de *S. fuscicauda* no son distinguibles de *S. meridanus* con base a cualquier carácter morfológico o biométrico y aves vecinas a la localidad tipo de *S. fuscicauda* comparten casi todos sus llamados con *S. meridanus*. Sugerimos tratar a *Scytalopus (griseicollis) infasciatus* como un sinónimo subjectivo más joven de *S. griseicollis*; y a *S. fuscicauda* como una subespecie de *S. meridanus*. A pesar de la alta similitud en caracteres de plumaje y biometría entre *S. meridanus* y *S. griseicollis*, todos sus llamados y cantos son 100% diagnosticable, soportando fuertemente el tratamiento de ambas como especies distintas (como re-defedinidos). Algunos especímenes de Colombia y Venezuela etiquetados en colecciones como "*S. meridanus*" en verdad corresponden a posiblemente dos *Scytalopus* no descritos de la zona montana baja, con un taxón en los Andes Orientales de Colombia y otra en los Andes de Venezuela. Especímenes colectados en la Serranía de Perijá son probablemente relacionados con *S. griseicollis* pero posiblemente son de otra especie o subespecie sin describir. Describimos *Scytalopus griseicollis aburriacantor* subsp. nov., de la Serranía de los Yariguíes en los Andes Orientales de Colombia. La nueva subespecie tiene un plumaje más oscuro y cola más larga que *S. griseicollis* y difiere al nivel de 85% en ciertos parámetros vocales medidos, comparados con poblaciones nominales ubicadas en el macizo principal adyacente de los Andes Orientales de Colombia. La nueva subespecie al parecer es endémica de la Serranía de los Yariguíes, restringida a cuchillas achaparradas y al ecotono páramo/bosque por encima de los 2450 m de elevación. En conclusión, recomendamos que los siguientes taxones sean reconocidos en este grupo: (i) Tapaculo de Matorral *S. griseicollis* (raza nominal; y *aburriacantor* subsp. nov.; y (ii) Tapaculo de Mérida *S. meridanus* (raza nominal; y *fuscicauda*).

[*] Proyecto de grado

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ABSTRACT

TITLE: TAXONOMY OF THE GREY-AND-ORANGE TAPACULOS (AVES: PASSERIFORMES: RHINOCRYPTIDAE) OF THE NORTHERN ANDES, WITH DESCRIPTION OF A NEW SUBSPECIES OF *SCYTALOPUS GRISEICOLLIS* FROM COLOMBIA[*]

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KEY WORDS: *Scytalopus*, tapaculo, new subspecies, species limits, Colombia, taxonomy

DESCRIPTION:

We analysed biometrics, plumage and voice to consider the taxonomy of four high elevation grey-and-orange Tapaculos *Scytalopus* taxa from the northern East Andes of Colombia and Mérida Andes of Venezuela: *S. griseicollis*, *S. infasciatus*, *S. meridanus* and *S. fuscicauda*. Individual plumage variation, including overall plumage darkness and vent barring, within both *S. griseicollis* and *S. meridanus* is substantial and each occurs across a broad elevational range. *S. infasciatus* is not diagnosable from *S. griseicollis* by voice, plumage or biometrics. *S. fuscicauda* skins are not diagnosable from those of *S. meridanus* and populations from near the type locality of *S. fuscicauda* are not certainly diagnosable for any of their calls from *S. meridanus*. We propose treating *Scytalopus (griseicollis) infasciatus* as a junior subjective synonym of *S. griseicollis* (including at subspecies level); and *S. fuscicauda* as a subspecies of *S. meridanus*. Although they have similar plumage and overlapping biometrics, all vocalisations of *S. meridanus* and *S. griseicollis* (each, as redefined) are 100% diagnosable by song speed, acoustic frequency and note shape, strongly supporting species rank for each of them. Some specimens from both Colombia and Venezuela labelled "*S. meridanus*" in collections relate to possibly two undescribed *Scytalopus* taxa of the lower montane zone that are apparently not closely related to *S. meridanus*. Specimens from the Perijá range are more likely related to *S. griseicollis* but may be of a further undescribed taxon. We describe *Scytalopus griseicollis aburriacantor* subsp. nov. from the Yariguíes range in the East Andes of Colombia. This new subspecies has darker plumage, a longer tail and differs at 85% level in acoustic frequency of its trills from nominate populations found in the adjacent main range of Colombia's Eastern Andes. The new subspecies is apparently an endemic of the Yariguíes massif, restricted to stunted ridges and paramo/forest ecotone above 2450 m elevation. In conclusion, we recommend that the following taxa should be recognised in this group: (i) Pale-bellied Tapaculo *S. griseicollis* (nominate race; and *aburriacantor subsp. nov*.), (ii) Merida Tapaculo *S. meridanus* (nominate race; and *fuscicauda*).

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INTRODUCTION

Despite some recent research and new taxon descriptions, the tapaculos *Scytalopus* Gould, 1836 of the northern Andes are among the most poorly understood bird taxa. Factors leading to the taxonomy of *Scytalopus* being particularly difficult, such as morphological homogeneity, collecting difficulties and the foxing of skins, have been widely discussed (Chapman 1915; Whitney 1994; Arctander & Fjeldså 1994; Krabbe & Schulenberg 1997 & 2003; and Cuervo *et al*. 2005). A landmark study, including detailed studies of habitat, range and voice of *Scytalopus* taxa principally in Ecuador, demonstrated that various morphologically similar but vocally different populations replace one another by elevation or in different habitats (Krabbe & Schulenberg 1997). Three new *Scytalopus* species have been described in this genus from Colombia in the last decade: Choco Tapaculo *S. chocoensis*, Upper Magdalena Tapaculo *Scytalopus rodriguezi* and Stiles' Tapaculo *Scytalopus stilesi* (Krabbe & Schulenberg 1997; Krabbe *et al*. 2005; Cuervo *et al*. 2005). Such descriptions, together with those of taxa from elsewhere in the Neotropics (Whitney 1994; Krabbe & Schulenberg 1997; Bornschein *et al*. 1998; Mauricio 2005; Raposo *et al.* 2006) and the elevation of many races to species status (principally in Krabbe & Schulenberg 1997; also Fjeldså & Krabbe 1990; Arctander & Fjeldså 1994; Ridgely & Tudor 1994; Bornschein *et al*. 1998; Coopmans *et al*. 2001; and Krabbe & Schulenberg 2003) have led to an increase in the number of recognised species from around 10 to over 40 since the 1990s.

Recent advances in *Scytalopus* taxonomy have largely resulted from research in the small Andean country of Ecuador (Krabbe & Schulenberg 1997). In Colombia, the Andes reach their greatest topographical complexity (Hilty & Brown 1986) and birds their greatest levels of diversity, intraspecific variation and terrestrial 'endemism' (Stattersfield *et al.* 1998; Orme *et al*. 2005; Phillimore *et al.* 2007). However, our understanding of the genus *Scytalopus*, particularly in the

East Andes, remains based largely on museum studies without vocal data by Chapman (1915), Hellmayr (1922) and Zimmer (1939) due to the lack of recent field studies. Further, in *Scytalopus* and many other little-studied genera of montane forest, the nature of intraspecific variation is not yet fully understood. It was recently predicted that the two recent descriptions of new *Scytalopus* from Colombia would be the first of a series of papers with descriptions of new taxa (Cuervo *et al*. 2005). This paper is indeed the first of several new *Scytalopus* descriptions from our studies of the genus in the East Andes (e.g. Donegan & Avendaño-C. submitted; Donegan *et al*. MS). In this paper, we analyse species limits and intraspecific variation in the grey-and-orange *Scytalopus*, a group of similar-looking species found at high elevations in the East Andes of Colombia and Venezuelan Andes – known formerly as *S. griseicollis*, *S. infasciatus*, *S. meridanus* and *S. fuscicauda* – with a view to recommending species limits in this group. The species *S. spillmanni*, which has a not dissimilar call to some of the aforementioned species, is also discussed. We also describe a new subspecies from Serranía de los Yariguíes in Colombia and lay the foundations for up to three further new taxon descriptions from within what is currently known as "*S. meridanus*".

1. STUDY AREA

1.1 GENERAL UBICATION

The East Andes are one of Colombia's three principal mountain ranges, extending from just north of the Equator to the Caribbean coast. They comprise one of the world's greatest centres of terrestrial avian endemism, with 35 bird species restricted to the range (Stattersfield *et al*. 1998). Serranía de los Yariguíes forms an isolated westward 100km long spur of the Cordillera Oriental, rising to around 3,400 m and isolated from the rest of the cordillera by the río Sogamoso valley to the north and east and to a lesser extent by depressions associated with the ríos Horta, Quirola and Opón and their tributaries to the south from around 2,500m elevation. Until recently, only small and sporadic bird collections existed from the Yariguíes region, mostly from lowland habitats (e.g. Borrero & Hernandez 1957; Romero 1983). High elevations had never been subject to ornithological study until recent surveys described in Donegan & Huertas (2005, 2006), Donegan & Briceño (2005), Donegan *et al*. (2005, 2007), Huertas & Donegan (2006) and Donegan & Avendaño-C (2006).

1.2 BACKGROUND

With E. Briceño and B. Huertas, TMD first sound recorded and observed greyish tapaculos of the *S. griseicollis* group in the Yariguíes mountains in stunted ridgetop habitat at a remote site Alto Cantagallos (2,450m, details below) in January 2004. In January 2005, TMD made further observations and sound recordings of the species at Lepipuerto (2,900m, details below), also in paramo and treeline habitat. Although the recorded voices differed in some respects from those of *S. griseicollis*, there was no type material. In July 2005, TMD, JEAC and others studied two sites in the highest elevations of Serranía de los Yariguíes (Filo

Pamplona at 3,200m, details below). We collected two birds and made a series of further sound recordings. In November 2006, JEAC obtained a further specimen at Alto Cantagallos.

2. METHODS

2.1 SPECIMENS EXAMINED

In order to investigate the relations of the new subspecies and distributions of all *Scytalopus* in Colombia, we made field observations of *S. griseicollis* in Santander, Boyacá and Cundinamarca departments of Colombia. We also inspected all northern Andean *Scytalopus* specimens at the following museums: Museo de Historia Natural, Universidad de la Salle, Bogotá, Colombia (MLS); Instituto de Ciencias Naturales, Universidad Nacional, Bogotá, Colombia (ICN); Colección Ornitologicá Phelps, Caracas, Venezuela (COP); Instituto Alexander von Humboldt, Villa de Leyva, Colombia (IAVH); Natural History Museum, Tring, UK (BMNH); and Museum National d'Histoire Nacional, Paris, France (MNHN). We were provided with photographs of types held at American Museum of Natural History (AMNH); Museum of Comparative Zoology, Harvard, United States (MCZ) and Museum für Naturkunde, Berlin (MfN). Specimens inspected are listed in Appendix 1 and include 189 skins labelled as either "*S. griseicollis*", "*S. infasciatus*", "*S. meridanus*" or "*S. fuscicauda*" (excluding specimens bearing such labels but clearly of other species). The following measurements were taken for each specimen: wing chord, tail length, (mm, to nearest 0.5 mm) tarsus length, culmen from skull to tip of upper mandible (mm, to nearest 0.1 mm) and, from specimen labels, mass (g). Data from birds in juvenile or immature plumage or undergoing primary moult were excluded.

2.2 VOCALISATION ANALYSES

We inspected various unpublished (Appendix 3) and published (see references) sound recordings. The following vocal parameters were measured: no. of notes in song; total song duration (s); average number of notes per second (by dividing

number of notes in song by song duration); maximum acoustic frequency of highest note (kHz); and maximum acoustic frequency of lowest note (kHz); and differences between the latter two measurements (kHz). Multiple calls were measured from single recordings where available. Data on numbers of recordings and calls, together with a gazetteer of recording localities, are presented for each taxon and call studied in Appendix 3. Following Isler *et al*. (1998), vocal differences were used to suggest species limits only if three or more diagnostic (non-overlapping) characters existed between populations.

2.3 STATISTICAL ANALYSES

Unequal variance (Welch's) t-test and Kolmogorov-Smirnov tests were applied on pairs of data for taxa being compared to assess whether statistically significant differences between samples exist, whilst catering for the possibilities that: (i) some populations may show greater individual variation than others; and (ii) some data (e.g. acoustic frequency data) may not be normally distributed. Diagnosability of vocal and biometric parameters was evaluated by considering overlaps between different taxa or populations.

3. RESULTS

3.1 UNRAVELLING THE *S. GRISEICOLLIS* / *S. INFASCIATUS* / *S. FUSCICAUDA* / *S. MERIDANUS* MORASS

Four poorly-known high elevation grey-and-orange *Scytalopus* taxa have been described from the East Andes of Colombia and adjacent Venezuelan Andes, the identity and validity of which have been controversial (Krabbe & Schulenberg 1997, 2003; Asociación Bogotana de Ornitología 2000). These taxa are: (i) Matorral (or Rufous-rumped or Pale-bellied) Tapaculo *S. griseicollis* (Lafresnaye, 1840) (East Andes of Colombia), (ii) Colombian (or Cundinamarca) Tapaculo *S. infasciatus* Chapman, 1915 (East Andes of Colombia); (iii) Merida Tapaculo *S. meridanus* Hellmayr, 1922 (Venezuelan Andes and, supposedly, Perijá range and elsewhere); and (iv) Lara Tapaculo *S. fuscicauda* Hellmayr, 1922 (northeastern Venezuelan Andes in Lara state).

3.1.1 Colombia's East Andes: Matorral Tapaculo *S. Griseicollis* And Colombian Tapaculo *S. Infasciatus.* Both *S. griseicollis* and *S. infasciatus* have been considered present in the East Andes of Colombia since the latter was described by Chapman (1915). *S. infasciatus* has historically and recently been treated as a species (e.g. Chapman 1915; Krabbe & Schulenberg 1997; Asociación Bogotana de Ornitología 2000; Salaman *et al*. 2001; Gill & Wright 2006). However, Krabbe & Schulenberg (2003) and some subsequent authors (Remsen *et al*. 2006; Salaman *et al*. 2007) have treated it as a subspecies of *S. griseicollis*.

The only unique distinguishing feature of *S. infasciatus* per the type description was relative darkness of underparts. Other small differences noted in the description, such as in barring of the vent, were considered probably due to age-

related variation (Chapman 1915). It was later hypothesised that some of the various calls given by *S. griseicollis* may have been calls of *S. infasciatus*, that the two taxa may separate by extent of barring on the underparts and that *S. griseicollis* was more common in dryer or secondary habitats, with *S. infasciatus* present in more humid habitats or better-conserved forest (Asociación Bogotana de Ornitología 2000).

The types of *S. griseicollis* (MCZ 76330 and 76331) are two "Bogotá" skins, an adult and a juvenile, and are typical of birds currently ascribed to this taxon in leading texts. Although it is never possible to be certain with "Bogotá" skins, these specimens most likely originated from near Bogotá itself, as *S. griseicollis* remains common in hills above Colombia's capital today. The type locality of *S. infasciatus* (AMNH 132328) is Paramó de Beltrán, on the eastern slope of the Eastern Andes in Cundinamarca department, some 15 km east of Bogotá, in Parque Nacional Natural (PNN) Chingaza. A recent plate of "*S. infasciatus*" (Krabbe & Schulenberg 2003) exaggerates considerably the darkness of the plumage of the type.

Recently collected eastern East Andes *Scytalopus* specimens (collected by JEAC in 2006 and others at ICN) do not differ significantly either in their plumage or biometrics from recent western East Andes specimens or material from the Bogotá region. Darker skins labelled *S. infasciatus* and lighter skins labelled *S. griseicollis* (other than from Serranía de los Yariguíes) are not distinguishable on the basis of their biometrics and do not separate by any known biogeographic divide. Biometric data combining measurements of birds assigned to both taxa in museums produced tight standard deviations for all measurements, similar to those produced for good species in the genus (see Appendix 2; Fig. 4). No statistically significant differences in biometrics were noted between western and eastern specimens. The considerable individual variation in the darkness of underpart coloration in skins appears to result from age-related individual variation. Similar variation in

underpart coloration is also evident in series of *S. meridanus* and *S. griseicollis* subsp. nov.

S. griseicollis taxa make three separate calls, all of which consist of rapidly repeated up-down strokes. These calls comprise: (i) short trills which rise and then fall in acoustic frequency (“trill”: "rriiiiiiaaaaa") (Fig. 6); (ii) rising churrs which only rise in acoustic frequency (“churr”: “zz-brrrrrrrrrr” or "brrrrrrrrrr") (Fig. 5); and (iii) curtailed monotonic reeling calls (“reeling call”: “zz-rrrrrrrrrrr…” or "rrrrrrrrrrr…") (Fig. 5). A comparison of sound recordings from eastern and western East Andes localities for trills and long reeling calls shows no statistically significant differences (Appendix 3; *t* and *K-S* tests for song length, notes/s, maximum frequency and minimum frequency, $p>0.05$ [$p>0.05$ for notes/s]) and substantial overlap (>85% for each parameter for such calls). Based on a small sample of four *S. griseicollis* and five *S. infasciatus* recordings, some average differences were apparently evident for churrs but even in this case for no parameter were 85% of recordings from different regions diagnosable. Given the extent of overlap of measured vocal parameters between “*griseicollis*” and “*infasciatus*” recordings, in light of guidelines for assessing species rank for suboscines developed by Isler *et al*. (1998), we concur with Krabbe & Schulenberg (2003) that *S. griseicollis* and *S. infasciatus* should be treated as conspecific; and go further in light of the lack of vocal, biometric or plumage differences and propose to treat *S. infasciatus* as a subjective junior synonym of *S. griseicollis*.

Although east-west geographical variation is Cundinamarca is not substantiated, north-south variation in *S. griseicollis* is evident and is a matter in need of further research. A recent sound recording (Fig. 6) and various specimens (Appendix 1; Fig. 1) confirm the presence of *S. griseicollis* in Tamá National Park, on both Colombian and Venezuelan sides of the national border. Biometric differences suggested by Figure 4 between Tamá and other skins are not statistically significant (*t* and *K-S*, $p>0.05$). Further north still, various specimens in museums,

mostly labelled "*Scytalopus meridanus*", originate from Serranía de Perijá and northern Norte de Santander department (Appendix 1). Although Krabbe & Schulenberg did not assign this population to any described taxon, Hilty (2003) treated it provisionally as *S. meridanus*. The voice of the Perijá population is unknown, meaning that it is impossible to make any strong conclusions about its possible relations or status. However, the near-continuity of Perijá populations with Tamá-Cucutilla populations of *S. griseicollis* would suggest that Perijá birds are more closely related to *S. griseicollis* than *S. meridanus*. Perijá specimens are longer-billed on average than *S. griseicollis* (*t* and *K-S*, $p<0.01$, although with considerable overlap); appear to show some small differences in dorsal plumage compared to both *S. meridanus* and *S. griseicollis* (Fig. 1); and come from a region that is isolated from nominate *S. griseicollis* populations by the narrow, low elevation section of the Andes in the Ocaña region. An undescribed *Scytalopus* taxon of unknown rank and uncertain affinities may be involved in the Perijá range.

Figure 1. Photographs showing various populations previously labelled "*S. meridanus*" from Venezuela.

From left to right: (i) *S. griseicollis* population from Perijá: COP 72580, Perijá, Zulia, Venezuela, 3000m, 6 July 1974; male; (ii) *S. griseicollis* COP 11101, collected at Paramo de Tamá, Venezuela (Colombian border), 2800m on 27 February 1941;

sex not determined; (iii) *S. meridanus* COP 49296 La Honda, Santo Domingo, Mérida, Venezuela, 6 December 1949; male; (iv) apparently undescribed species COP 65395, La Azulita, Mérida, 2300m, 25 November 1959; male. Note the morphological similarities of the first three skins. Birds represented by the second and third skins have strikingly different voices from one another. Photographs corrected for greyscale on Photoshop. Photograph © B. Huertas, taken at COP.

3.1.2 Venezuelan Andes: Merida Tapaculo *S. Meridanus* And Lara Tapaculo *S. Fuscicauda.* Recent authors recognise two grey-and-orange *Scytalopus* in the Venezuelan Andes: Merida Tapaculo *S. meridanus*, found across much of the range; and Lara Tapaculo *S. (griseicollis) fuscicauda*, found exclusively in Lara state to the Lara/Trujillo border (e.g. Krabbe & Schulenberg 1997, 2003; Hilty 2003). *S. fuscicauda* is generally described as a high elevation bird with no barring on its orange underparts (Hellmayr 1922; Krabbe & Schulenberg 2003; Hilty 2003). *S. meridanus* has been considered a species with barred underparts, with higher elevation records having been doubted and some texts illustrating a rather dark-plumaged bird (Fjeldså & Krabbe 1990; Krabbe & Schulenberg 2003; Hilty 2003). On a basis of sound recordings presented by Boesman (1999), Krabbe & Schulenberg (2003) thought that *S. fuscicauda* might be synonymous with *S. meridanus* but nonetheless elevated it to species rank on a basis of it clearly not being related to *S. griseicollis*. BirdLife International (2007) recently declined to recognise *S. fuscicauda*, based on some of the data presented herein.

Our analysis of specimens suggests that two species or distinctive colour morphs exist within what is currently referred to as "*S. meridanus*" in the Mérida range (as discussed further below). However, as suspected by Krabbe & Schulenberg (2003) and as explored further in this section, *S. meridanus* and *S. fuscicauda* should be treated as conspecific.

The type of *S. meridanus* (AMNH-492377) is a rather grey *Scytalopus* with a strongly-barred orange vent. The specimen label states that it was collected at 4,000m elevation at La Culata in Mérida state (08°45'N; 71°05W, per Paynter 1982). Another specimen from this locality was collected at 3,000m, which seems more plausible (Appendix 1). The *S. fuscicauda* type was collected by Carriker at Paramo de Rosas, close to the Trujillo state border in Lara state (09°35'N, 70°07'W, 3,245 m, per Paynter 1982) and differs from the *S. meridanus* type in having no strong barring on the vent (Hellymar 1922; Fjeldså & Krabbe 1990; Hilty 2003). Hellmayr (1922) provisionally included within the *S. meridanus* species grouping certain specimens from Santa Marta, southern Colombia and Peru (whilst noting that such specimens might refer to other taxa is now known to be the case). Hellmayr also included within *S. meridanus* at least one specimen from south-western Lara state (Anzoátegui, Lara: 09°36'N 69°54'W, per Paynter 1982). One BMNH skin labelled "*S. fuscicauda*" (1914.11.26.507), which is likely to have been inspected by Hellmayr, is indistinguishable from other skins labelled of this species at BMNH lacking strong barring was collected at La Culata, Mérida, the type locality of *S. meridanus*.

Individual morphological individual variation within the *S. meridanus* series at COP and elsewhere is remarkable. Specimens with strong barring on the vent have been collected in each of Táchira (e.g. COP-24549), Mérida (e.g. COP-64271) and Trujillo (e.g. COP-26179) states and from low (e.g. COP-62231, 2200m) and high (e.g. COP-64271, 3300m) elevations. Specimens without strong barring are less frequent in collections but are found in series from Mérida (COP-64261), Trujillo (COP-19963) and Lara (*S. fuscicauda* type, per Hellmayr 1922) states and from low (COP-24548, 2,400m) to high (COP-64261, 3,300m) elevations. Birds with intermediate strength of barring are also found in all states, with no discontinuity in this plumage feature. Strongly barred and less strongly barred or unbarred birds thus do not appear to follow any general elevational or geographical pattern. Biometric data of all *S. meridanus* and *S. fuscicauda* skins produces tight standard

deviations comparable with those produced for taxa currently considered to be good species in the genus (Appendix 2). Although degrees of freedom are small, *t* and *K-S* tests shows no statistically significant differences in wing, tail, tarsus or bill length between specimens labelled as of these two taxa ($p>0.05$). It seems implausible that two morphometrically and vocally indistinguishable *Scytalopus* species would co-occur across such a broad elevational and geographical range. Although we have noted sympatry of some morphologically different *Scytalopus* in our studies in Colombia (notably, Spillmann's Tapaculo *S. spillmanni*, which occurs together with other taxa in Colombia's Central and East Andes), Krabbe & Schulenberg (1997) generally found sharp elevational or habitat replacements to be frequent in this genus.

S. meridanus has an unusually wide elevational range, with skins from 2,200m to 4,000m and observations in PN Yacambu in Lara state down to 1,600 m (P. Boesman *in litt*. 2006). Such an elevational range is similar to that of *S. griseicollis* in the East Andes (found from 2,450 m in forest (Yariguíes, below) or 1,300 m in secondary growth (recent sound recording by A. Hernández-J. in IBA La Judia, Santander) up to 3,900m (ICN 12010 at Laguna de Chisacal, Cundinamarca). In a region further from the equator, a species with apparently similar habitat requirements such as *S. meridanus* could be expected to have a similarly wide elevational range in suitable habitats.

Most of the vocalisations given by "*S. meridanus*" and "*S. fuscicauda*" are indistinguishable between populations in Táchira, Mérida, Trujillo and Lara states, including the 'trill' (represented by sonagrams 68/71 in Krabbe & Schulenberg 1997) and some call notes (e.g. sonagrams 69/72). 'Reeling calls', similar to that of sonagram 70, have also been recorded throughout Venezuelan Andes. Unlike in *S. griseicollis*, there is considerable variation in delivery speed, with calls often including short gaps and having notes delivered in groups of two, three or more (cf. some calls of *S. parkeri*). In Táchira, Mérida and Trujillo states, reeling calls often

have introductory notes which are more drawn-out (longer in duration) than notes comprising the reeling call, though in one recording there is no such introduction. The two recordings we have inspected of reeling calls from Lara state (from whence "*S. fuscicauda*") have less drawn out (shorter) introductory notes (noted by P. Boesman *in litt*. 2006). As variation in introductory phrases to reeling calls are evident within *S. griseicollis*, we treat such differences with caution: a greater sample of *S. meridanus* recordings is needed to assess whether these differences are a feature of individual or geographical variation. It is possible that different call introductions have different communication functions. Even if such differences in introductory notes are borne out with a greater sample, vocal parameters of song speed and acoustic frequency overlap considerably between western and eastern recordings for reeling calls. Suboscines which are morphologically indistinguishable and which overlap substantially in vocal parameters are generally treated as conspecific (Isler *et al*. 1998: e.g. approach to Paramo Tapaculo *S. canus* and Northern White-crowned Tapaculo *S. atratus* taxa in Krabbe & Schulenberg 1997).

In conclusion, no morphometric, biogeographic, plumage or vocal data supports the treatment of *S. fuscicauda* as a species. Further, such a treatment should not be regarded as a "status quo" (*contra* e.g. Remsen *et al*. 2007) given that *S. fuscicauda* was lumped with either *S. magellanicus* or *S. griseicollis* until 2003, including by Hilty (2003) in the leading field guide for the region. Whilst we agree with Krabbe & Schulenberg (2003) that *S. fuscicauda* is not conspecific with *S. griseicollis*, the best approach presently would be to treat it as a subspecies of *S. meridanus*. Although detailed vocal studies are needed to confirm this, the two may prove in time to be subjective synonyms.

S. fuscicauda and *S. meridanus* were described contemporaneously by Hellmayr (1922). Neither therefore has priority in the event that they are treated as conspecific (International Code for Zoological Nomenclature, Article 23). Pursuant

to ICZN Article 24A, it is recommended that the name, spelling or nomenclatural act that will best serve stability and universality of nomenclature should be adopted. Universality considerations could be thought to include "position precedence" (under ICZN Article 69A.10 which applies to the fixation of type species for genera and in certain broadly analogous situations, all other things being equal). Such an approach would favour use of the species name that appears first in Hellmayr (1922) which is *S. fuscicauda*. However, all other things are not equal here. *S. meridanus* is the name which has been assigned to *Scytalopus* occurring in most of the Venezuelan Andes in three recent landmark publications (notably, Krabbe & Schulenberg 1997 and 2003 and Hilty 2003). We therefore formally propose that the name *S. meridanus* should be given precedence over *S. fuscicauda* in the event that the two are considered conspecific or synonymous (for the purposes of ICZN Article 24.2). Such an approach encourages nomenclatural stability.

3.1.3 Species Limits Between *S. Meridanus* And *S. Griseicollis.* Due to morphological similarities, questions have been raised in the past over whether all populations of grey-and-orange tapaculos occurring in the Colombian and Venezuelan Andes should be treated as conspecific (Krabbe & Schulenberg 1997). However, it recently became evident that populations in the Venezuelan and East Andes have a different voice from one another (Boesman 1999; Fig. 5) leading to their treatment as different species in most recent publications (e.g. Krabbe & Schulenberg 2003; Remsen *et al*. 2007). Data presented in Appendix 2 shows the trills and reeling calls of *S. griseicollis* taxa and *S. meridanus* taxa (as redefined above) to be 100% diagnosable from one another on a basis of song speed and maximum acoustic frequencies, whilst note shape is also rather different (Fig. 5). *S. meridanus* reeling calls are also typically much longer in duration than those of *S. meridanus* and vary in speed of delivery, often slowing over time and then delivered in groups of 2-7 notes with spaces between them (cf. generally uniform delivery in *S. griseicollis*) and sometimes include drawn-out introductory notes of a

different note shape to the “zz” sometimes in *S. griseicollis* recordings. No call comparable to the churrs of *S. griseicollis* are found in *S. meridanus*. *S. meridanus* rather has at least two other calls not found in *S. griseicollis*: long repetitions of upstrokes; and short calls similar in shape to notes or introductory notes of its other calls but sometimes longer in duration.

Another species possibly related to *S. griseicollis* and *S. meridanus* is Spillmann’s Tapaculo *S. spillmanni*, which has a similar song consisting of rapid up-down strokes. *S. spillmanni* has recently been discovered in the East Andes of Colombia where an undescribed subspecies is present which is considerably darker in plumage than other Colombian populations (Donegan et al. 2007). This and other populations of *S. spillmanni* are easily diagnosable from *S. griseicollis* by their plumage (darker grey, darker rufous on vent) and are larger and heavier on average (but not diagnosably). In Serranía de los Yariguíes, *S. spillmanni* and *S. griseicollis* were sympatric but replaced one another in different habitats, with *S. spillmanni* exclusively in montane forest, often associated with bamboo, and *S. griseicollis* at locally higher elevations in paramo and subparamo. The only songs we have recorded to date of the East Andes population of *S. spillmanni* are rising churrs and reeling calls which are structurally identical to one another (differing only in call duration). *S. spillmanni*’s call is diagnosable from that of *S. griseicollis* only by its higher maximum acoustic frequency; and from that of *S. meridanus* only by its faster song speed (Appendix 2).

Vocalizations in suboscines such as *Scytalopus* are considered to be innate and stereotypical (Kroodsma 1984; Whitney 1994; Cuervo *et al*. 2005). Species rank for each of *S. meridanus* and *S. griseicollis* is supported strongly by diagnosability of vocal characters in all calls given by both species, following Isler *et al*. (1998)’s approach for assessing species rank for allopatric populations using vocal characters. It is of note that *S. griseicollis* and *S. meridanus* differ diagnosably in their voice in more characters than do sympatric *S. spillmanni* and *S. griseicollis*

(which are certainly good species with respect to one another) - supporting species rank for all three of them under the Helbig *et al*. (2002) biological species concept.

3.1.4 Undescribed Lower Montane *Scytalopus* In Colombia's East Andes And The Venezuelan Andes. Our studies in the field and of skins reveal the presence of possibly two undescribed *Scytalopus* at lower montane elevations (around 2000 m) of Colombia's East Andes and the Venezuelan Andes, all specimens of which have been labelled "*S. meridanus*" or "*S. femoralis*" in museums (Donegan *et al*. 2007). One such population is found in the East Andes of Colombia (see further Donegan *et al*. 2007 and specimens listed under "*S. rodriguezi* undescribed subspecies or related but undescribed species" in Appendix 1). This population is apparently not closely related to either *S. meridanus* or *S. griseicollis*, having darker plumage and a different voice. Separately, four COP specimens collected at 2200-2400m elevation in the Venezuelan Andes (listed in Appendix 1) have a darker shade of grey plumage overall, a darker and browner shade of rufous on the underparts (which are consistently strongly barred: Fig. 1, plate of "*S. meridanus*" in Hilty 2003) and a longer tail than *S. meridanus* (*t* and *K-S*, $p<0.01$, d.f.=2). These specimens appear likely to be of an undescribed colour morph or species (possibly related to *S. spillmanni* or *S. rodriguezi*). The (valid) description of *S. rodriguezi* could be regarded with hindsight as having been rather fortuitous in light of similar-looking, apparently related, birds labelled "*S. meridanus*" in collections and leading texts. The populations discussed in this section will be considered in further detail in other publications, as they are not "grey-and-rufous" *Scytalopus*, as defined herein.

3.1.5 Notes On Vernacular Names. The name "Matorral Tapaculo" was proposed for *S. griseicollis* by Krabbe & Schulenberg (1997) and was used by Krabbe & Schulenberg (2003), Restall *et al*. (2006) and Remsen *et al.* (2007). Other possible vernacular names include "Rufous-rumped Tapaculo" (Hilty 2003; Gill & Wright 2006), "Pale-bellied Tapaculo" (Asociación Bogotana de Ornitología 2000),

“Colombian Tapaculo” (the traditional name for *S. infasciatus*) and “Cundinamarca Tapaculo” (used by Gill & Wright 2006 for *S. infasciatus*). “Rufous-rumped” has only been used for a Venezuelan population which we do not treat as part of *S. griseicollis*. “Pale-bellied” is a good descriptive name for the redefined species, but has been used in only one regional publication of which we are aware. As for the geographical names, these are hardly informative as various other Tapaculos occur both in Colombia and Cundinamarca and *S. griseicollis* is not endemic to either. Use of “Matorral” for the combined group would follow the majority of recent leading texts, but is based on the formerly assumed separation of *S. griseicollis* and *S. infasciatus* by forest and scrub habitat. ‘*Matorral*’ is a Spanish (not English) word and an important habitat of *S. griseicollis* (as redefined herein) is primary páramo and subpáramo of the East Andes, making this name somewhat misleading. “Pale-bellied Tapaculo” is therefore perhaps the best name for *S. griseicollis* following the taxonomic revisions herein.

If *S. fusciscauda* is considered conspecific with *S. meridanus*, as proposed, three vernacular names are available. "Merida Tapaculo" is the traditional name for *S. meridanus*; "Lara Tapaculo" has been used for *S. fuscicauda* when treated as a species (Krabbe & Schulenberg 2003; Gill & Wright 2006; Restall *et al*. 2006); and "Rufous-rumped Tapaculo" was used by Hilty (2003) for “*S. griseicollis fuscicauda*” in Venezuela. The name "Merida Tapaculo" is preferable as it is the name already in use for the taxon occurring in most of the region; also, it refers to the mountain range as well as one of the political units in which the species is found. "Rufous-rumped" is a fairly redundant name that could be used to describe many *Scytalopus* taxa and was recently used for *S. griseicollis*. "Lara" would not be appropriate in light of the proposed treatment of *S. fuscicauda* as a subspecies of *S. meridanus* and wider range of the combined species.

3.1.6 Recommendations. In conclusion, we recognise the following grey-and-orange *Scytalopus* of the East Andes of Colombia and Venezuela Andes:
(a) Pale-bellied Tapaculo *S. griseicollis*. Subspecies: (i) nominate; (ii) *aburriacantor subsp. nov.* described herein. We treat "*S. infasciatus*" as a subjective junior synonym of *S. griseicollis*. The status of Tamá and (particularly) Perijá populations requires further research.
(b) Merida Tapaculo *S. meridanus*. Subspecies: (i) nominate; and (ii) *fuscicauda*.

3.2 DESCRIPTION OF A NEW SUBSPECIES OF *SCYTALOPUS GRISEICOLLIS* FROM THE YARIGUÍES MOUNTAINS

The Serranía de los Yariguíes population of *S. griseicollis* shows small plumage and biometric differences from populations in the main East Andes and differs significantly but non-diagnosably in some vocal parameters. We describe this population as a subspecies of *S. griseicollis* and propose the following name:

Scytalopus griseicollis aburriacantor subsp. nov.

3.2.1 Holotype

Figure 2. The holotype of *S. g. aburriacantor* (B. Huertas/Proyecto YARE).

Adult male no. ICN 35609; collected by T. Donegan & J. Avendaño-C. and prepared by J. Avendaño-C. (field number JEAC 297) on 13 July 2005 in paramo at Filo Pamplona above La Aurora, vereda San Isidrio, Municipality of Galán, Santander Department, Colombia (06º38'N; 73º24'W; 3200 m) on the eastern slope of the Yariguíes massif. Deposited at Instituto de Ciencias Naturales, Universidad Nacional, Bogotá, Colombia. Tissue samples (heart) and a skeleton were deposited at the Centro de Innovación en Biotecnología y Biología Molecular (CINBIM) in Universidad Industrial de Santander (UIS), Bucaramanga, Colombia and at Universidad de los Andes.

3.2.2 Diagnosis. *Scytalopus griseicollis aburriacantor* is a rather grey *Scytalopus*, exhibiting the typical characteristics of the genus, including: a fairly sharp, laterally compressed bill with relatively high culmen; nares covered by relatively conspicuous operculum; short and somewhat erect feathers in lores; soft, short, concave and rounded wings with 10 primaries; relatively short and graduated tail with 10 rectrices (within range for the genus) with the outermost rectrices shorter than the others; tail shorter than the wing; large and strong feet with distinct taxaspidean tarsal scutellation; hind claw strongly curved and shorter than the digit; uncolorful plumage with soft feathers; non-ossified skull; a rather broad and spherical thoracical cavity; dark, reddish/brown iris; dark plumage characterised by only black, grey, white or brown pigmentations in feathers; dark and relatively rather long tarsi; vocalisations consisting of simple scolds, rattles, whistles or trills; high elevational distribution; habits skulking in lower undergrowth up to c. 3m above ground level; and (based on stomach contents) an insectivorous diet (Ridgway 1911; Krabbe & Schulenberg 1997; Cuervo *et al*. 2005).

The new taxon appears to be most closely related to *S. griseicollis* and *S. meridanus*. The latter two species also have overall rather grey plumage and orange-brown vent, calls involving unmusical trills, and a paramo and subparamo habitat of the north-easternmost extensions of the tropical Andes: the East Andes

of Colombia and Venezuelan Andes. Preliminary molecular studies show one individual of *S. g. griseicollis* and one of *S. g. aburriacantor* to share the same mtDNA haplotype for one molecular marker (the second subunit of the NADH deshydrogenase gene: ND2) (C.D. Cadena in litt. 2007).

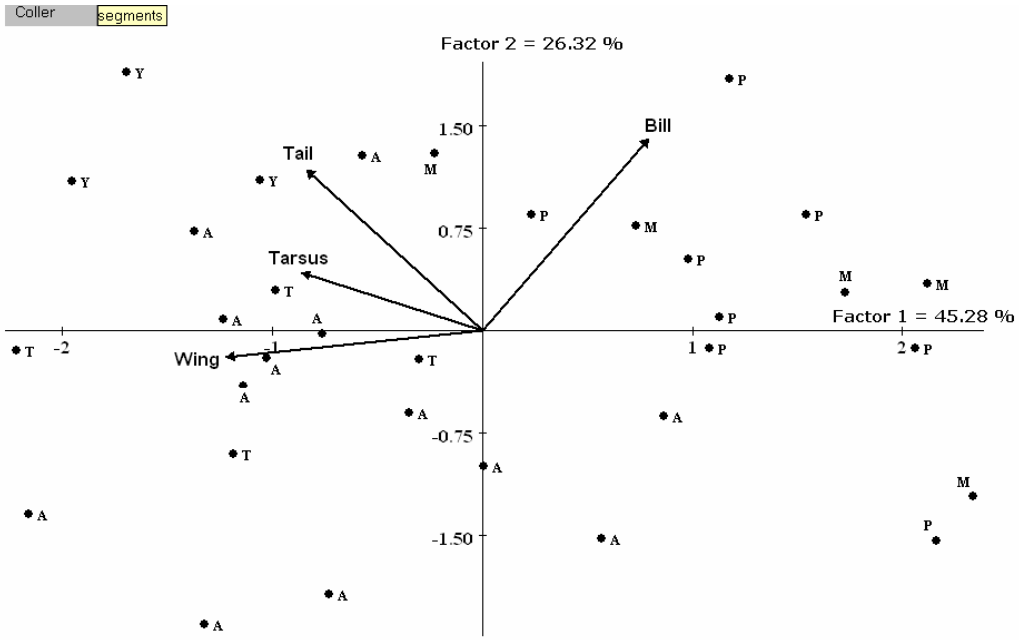
S. g. aburriacantor differs from nominate *S. griseicollis* in having: darker grey underparts; a darker (less brown) back and tail; darker rufous vent (Fig. 3); average longer tail (*t* and K-S for males: $p<0.01$) and, possibly, average longer wing, tarsus and bill than populations of the nominate subspecies (Appendix 2), although the latter measurements do not produce statistically significant results. Yariguíes specimens cluster separately from those of other East Andes populations in PCA analysis (Fig. 4). 100% of the *S. g. aburriacantor* sample has a tail length of 44 mm or more; whilst 93% of *S. g. griseicollis* population (including longer-tailed northern specimens) have a tail length of 43.5 mm or less. Acoustic frequency of trills and churrs is lower than in the nominate population, with 85% diagnosability for trills. We did not hear long reeling calls of up to 15 seconds as given by nominate *S. griseicollis* at any of our sites. Specimens and sound recordings of nominate *S. griseicollis* from the East Andes at sites adjacent to Serranía de los Yariguíes at Suratá in Santander (ICN 36121; J. Avendaño-C. sound recordings) and the Boyacá/Santander border at Arcabuco (ICN 10852; R. Chavarra & J. Zuluaga sound recordings), each of which are *c*.50 km from Serranía de los Yariguíes in the main section of the East Andes are consistent with those from elsewhere, discounting the possibility of clinal variation causing these differences.

Figure 3. Left: photographs of (left to right) and four recently-collected (within last 5 years) *S. griseicollis:* (i) ICN-34492 (female, Cundinamarca, Bosque de Toma, Cerros Orientales de Bogotá, 3050m, collected on 1 April 1993 by S. Guttiérez & S. Rojas, labelled "*griseicollis*" and an example of one of the lighter specimens); (ii) ICN-31235 (male, Cundinamarca, Chingaza, Piedras Gordas; collected by F.G.

Stiles on 1 November 1991, a relatively dark bird formerly labelled "*infasciatus*" and possibly an immature); (iii) immature paratype *S. g. aburriacantor*; and (iv) adult holotype *S. g. aburriacantor*. Right: dorsal view of (left to right): (i) *S. g. aburriacantor* holotype; (ii) *S. g. aburriacantor* paratype; (iii) ICN-UN 34780 (male, Cundinamarca, Bogotá, Cerros Orientales, La Aurora, collected on 15/11/2003 by F.G. Stiles); (iv) ICN-UN 34492 (see (i) above); (v) 31235 (see (ii) above); (vi) ICN-UN 19623 (male, Cundinamarca, Bogotá, Monserrate, collected by P. Bernal on 19 June 1968). Photographs by T. Donegan.

S. g. aburriacantor can be distinguished from *S. meridanus* of the Venezuelan Andes by the new taxon's average longer wing and tail, darker back, darker shade of orange/rufous on the vent and voice. *S. g. aburriacantor* can be distinguished from all other *Scytalopus* by its relatively light grey plumage, reddish orange rump and voice. Compared to species with which it is sympatric or parapatric, *S. spillmanni*, *S. rodriguezi sp.*, *S. latrans*, *S. atratus* and *S. sp.* are all darker tapaculos and have rather different vocalisations.

Figure 4. Principal Component Analysis using bill, tail, tarsus and wing data for adult males only of *S. griseicollis* ("A": all East Andes north to Santander), *S. meridanus* ("M": all Venezuelan Andes), *S. griseicollis subsp*. of Perijá ("P": all Perijá range of East Andes), *S. griseicollis* from the Tamá region ("T": East Andes in Norte de Santander, Colombia and Apure, Venezuela) and *S. g. aburriacantor* ("Y": isolated spur of East Andes).



3.2.3 Description Of The Holotype. A description with colour nomenclature follows Munsell (1977; 2000): bill black (not coded); ventral proximal lower mandible tipped slightly lighter at base (Gley 1 7/N); iris dark brown (10R 3/3); head, mantle and tail dark grey-brown (7.5YR 2.5/2); underparts to breast grey (Gley 1 3/N), becoming slightly lighter (Gley 1 4/N) on lower belly; wing coverts and flight feathers dark grey (7.5YR 2.5/2) with tertials tipped ochraceous brown (5YR 3/4), with dark grey (7.5YR 2.5/2, but darker than other wing feathers) subterminal bar; wing rounded with wing point hard to discern but close to fifth (sixth from outermost) primary; no emarginations or primary notches noted; flanks and

undertail coverts ochraceous brown (7.5YR 3/4) barred black (not coded) on flanks; rump brown (5YR 3/4) thinly barred dark grey (7.5YR 2.5/2); tarsus reddish dark grey (5YR 4/3) frontally, behind lighter (10R 3/1); Foot soles greyish yellow (2.6Y 8/2). All feathers fresh with no moult noted; testes rather enlarged (left testis: 5.4 x 2.2 mm; right testis 4.2 x 2.7 mm); stomach contents not determined. Measurements of holotype (for feathers to nearest mm; for others to nearest 0.5 mm): maximum flattened wing (field) 62, wing chord (skin) 58, tail 45, tarsus 22.5, full culmen 13.5, exposed culmen 11.0; mass 18.0g.

3.2.4 Paratypes And Other Material. We assign the following specimens as paratypes: (1) Immature male no. ICN 35610; collected by T. Donegan & J. Avendaño-C. and prepared by T. Donegan on 14 July 2005 at the Filo Pamplona type locality. Tissue samples (heart) and a skeleton have also been deposited at UIS. (2) Adult male no. ICN 36175, collected and prepared by J. Avendaño-C. (JEAC 377) on 12 November 2006 on a stunted ridge above at Alto Cantagallos, above Santo Domingo farm, Municipality of San Vicente de Chucurí, Santander Dept, Colombia (06º48'N; 73º21'W; 2450 m) on the western slope of the Yariguíes massif. Tissue samples (heart and liver) have also been deposited at UIS and Universidad de los Andes.

A series of sound recordings of *S. g. aburriacantor* have been deposited at the British Library in London and at Instituto Alexander von Humboldt's Banco de Sonidos Animales. Some will be made available on www.xeno-canto.org following publication of this paper.

3.2.5 Variation In The Paratypes And Other Individuals Encountered. The Pamplona paratype is also a male but had smaller testes (left: 3 x 1.5mm; right: 2.5 x 1.5mm), suggesting a younger bird. It has darker grey underparts than the adult (Gley 1 3/N), not lightening so significantly on the lower belly; and more brownish (7.5YR 3/4) plumage on the upper mantle, neck and crown. Measurements are as

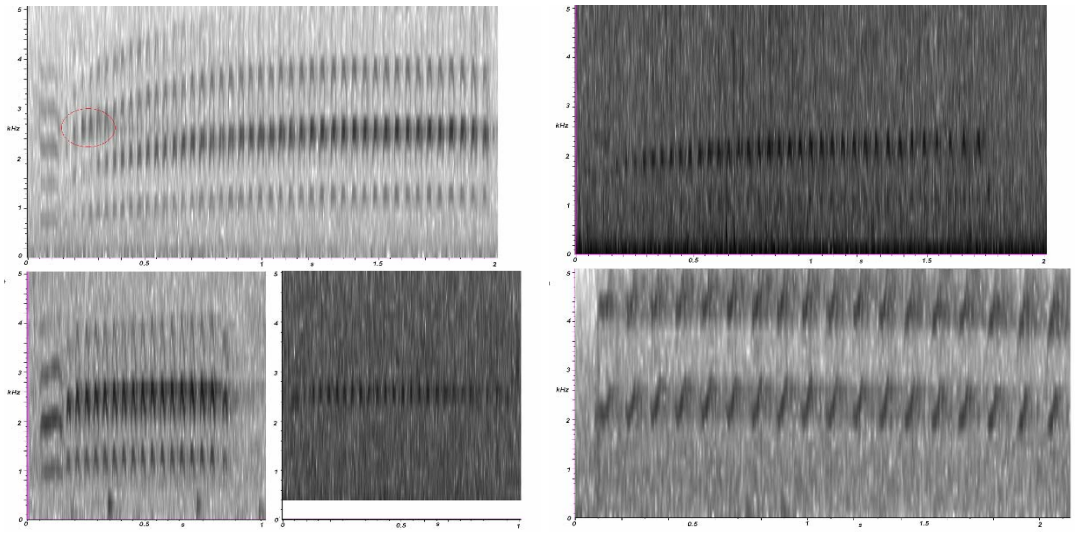
follows (mm): maximum flattened wing (field) 61, wing chord (skin) 56, tail 44, tarsus 22.0, full culmen 13.5, exposed culmen 11.0, mass 17.5 g. Stomach contents included Coleoptera exoskeleton remains.

The Alto Cantagallos paratype is also a male but with rather large testes (4.6 x 2.7mm; right: 4.2 x 3.2mm). It is similar to the holotype in its upperpart and underpart coloration but lacks black barring on flanks and undertail coverts. Barring on the vent is a character which is also variable in nominate *S. griseicollis* (Chapman 1915) and *S. meridanus* (see above). Measurements are as follows (mm): maximum flattened wing (field) 57, wing chord (skin) 57, tail 44, tarsus 23.0, full culmen 13.2, exposed culmen 9.3.

We and other fieldworkers (E. Briceño and B. Huertas) have observed individuals at sufficiently close quarters on approximately 20 occasions during three weeks' total fieldwork at three study sites at which the species was relatively common, all of which were consistent with the type series.

3.2.6 Vocalisations. We made over 40 separate recordings of calls of *S. g. aburriacantor* involving over 120 vocalization events. We have compared our recordings with recordings of *S. griseicollis* from the Eastern Cordillera in westernmost Venezuela (Apure state) and in Colombia from Norte de Santander, Santander, Boyacá and Cundinamarca departments (localities in Appendix 3). We recorded three separate calls of *S. g. aburriacantor*. The 'trill' ("*rriiiiiiaaaaa*") (Fig. 6) comprised *c*.70% of recordings; (ii) rising 'churrs' ("*brrrrrrrrrr*") (Fig. 5) comprised *c*.25% of recordings; and curtailed monotonic 'reeling calls' ("zz-rrrrrrrrrrrrrrrrr" or "*rrrrrrrrr*") (Fig. 5) comprised (<5% of recordings). Parameters of all three of these calls for *S. griseicollis*, *S. g. aburriacantor* and, where comparable, *S. meridanus*, are set out in Appendix 3, together with a gazetteer of recording localities. Analyses of acoustic frequencies are based on the loudest notes on sonograms, those of the first overtone.

Figure 5. Sonograms of (i) above left: extract of churr bout of *S. griseicollis* (JEAC recording Suratá, Santander, 15 March 2006, at 3300 m elevation at La Pajita Farm, Vereda Bucaré, Santander) with accentuated first overtone at start of call circled in red and flat "zz" at start of call; (ii) above right: same call in *S. g. aburriacantor* (TMD recording at Filo Pamplona type locality, Yariguíes, July 2005) which lacks the accentuation of the second overtone but has the initial "zz", barely visible on sonagram at start of call; (iii) bottom left: curtailed reeling call of *S. griseicollis* from Chingaza, Cundinamarca, Colombia (J. Parra recording), also with introductory "zz"; (iv) middle left: sonogram of curtailed "reeling call" of *S. g. aburriacantor* with initial "zz" (TMD recording, Lepipuerto, Yariguíes, January 2005); (vi) bottom right: slower and higher frequency trill of *S. meridanus* in Venezuela (Boesman 1999: Paramo de Batallón, Táchira state, Venezuela, 2700-2900 m; A17A_2C.WAV).



Trills are repeated in long series of up to 20 trills, with irregular intervals (typically 1-5s). Nominate *S. griseicollis* trills average higher frequency than those of *S. g. aburriacantor* (Fig. 6) (*t* and *K-S*, $p<<0.01$). For *S. g. aburriacantor*, 62.5% of recordings do not include any calls which are >3.5 kHz; and 75.0% of *S. griseicollis* recordings do not include any calls that are <3.5kHz. 85.4% of individual *S. g.*

aburriacantor calls analysed were < 3.5kHz, whilst 84.0% of all *S. g. griseicollis* recordings analysed were >3.5 kHz. The sample for this call involves multiple recordings from different regions for each taxon and the extent of overlap is relatively small, suggesting that subspecies rank is not inappropriate for *S. g. aburriacantor*.

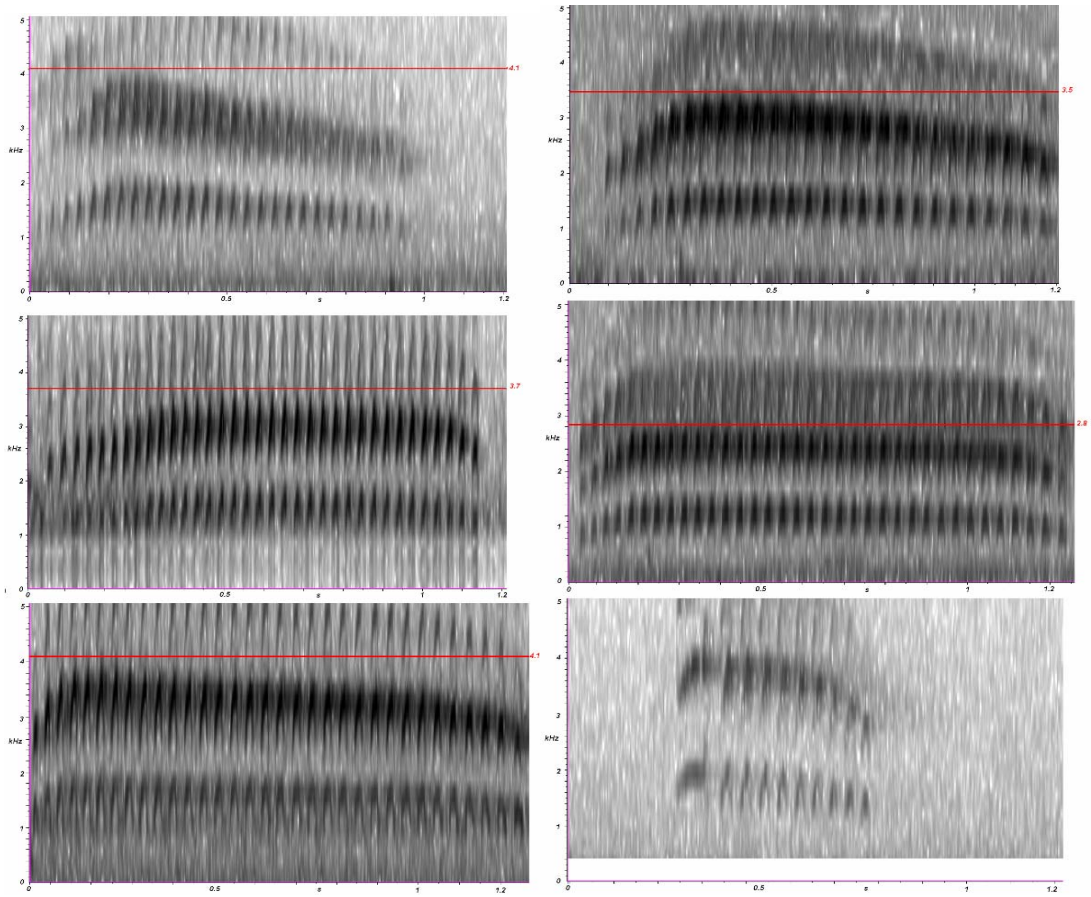
As in nominate *S. griseicollis*, churrs are given in bouts, often becoming longer in duration sequentially, and sometimes include an introductory "zz". *S. griseicollis* (but not always) often includes brief accentuation of the second overtone at the start of the call “[zz-]trbrrrrrrrrrrr” (Fig. 6: see also sonagram 74 in Krabbe & Schulenberg 1997), a feature not present in any of our recordings of churrs of *S. g. aburriacantor*. As for the trill, *S. g. aburriacantor* averages lower acoustic frequencies than nominate *S. griseicollis*, though not diagnosably (<50% diagnosability for recordings at <>2.6kHz).

Reeling calls in nominate *S. griseicollis* last up to 15s (Krabbe & Schulenberg 2003), whilst we never heard or recorded reeling calls of *S. g. aburriacantor* of >3s duration at any of our sites and only sound recorded calls of <2s. Although the lack of long calls over 15 days’ fieldwork was noteworthy, this does not necessarily mean that *S. g. aburriacantor* never makes longer reeling calls. Other than average call length, *S. g. aburriacantor*’s reeling calls are structurally similar to those of *S. griseicollis*. Some reeling calls of *S. g. aburriacantor* had a short, flat introductory note "zz" before the trill whilst others did not.

Finally, a harsh, unmusical rattle has apparently been recorded once for each of *S. g. griseicollis* and *S. g. aburriacantor*, but not certainly ascribed to an individual of the species. With only one recording for each taxon, we regard such calls as unconfirmed and do not comment on differences or parameters.

Figure 6. Sonograms of trills of *S. griseicollis* and *S. g. aburriacantor*. Left three trills are a sample showing variation in frequency and structure of this call given by

S. griseicollis. Top left: PNN Tamá, Apure, Venezuela (C. Parrish recording no. 6079 on www.xeno-canto.org); Middle left: PNN Chingaza, Cundinamarca, Colombia (J. Parra-B. recording); Bottom left: Rogitama, Boyacá, Colombia (J. Zuluaga recording). Above right two trills are indicative of the variation in frequency and structure in this call for *S. griseicollis aburriacantor*. Top right: Filo Pampona, Serranía de los Yariguíes (TMD recording); Middle right: Alto Cantagallos (TMD recording). Although there is some overlap in frequency, note the generally lower frequency of the second overtone in *S. griseicollis aburriacantor*. Most *S. g. griseicollis* recordings attain frequencies of 3.5 kHz or more, whilst few *S. g. aburriacantor* recordings do. Bottom right: curtailed trill of nominate *S. griseicollis* in Suratá, Santander (JEAC recording, 15 March 2006, 3,300 m, La Pajita Farm, Vereda Bucaré, Santander).



S. meridanus calls are very different from those of nominate *S. griseicollis* and *S. g. aburricantor*, consisting principally of upstrokes, rather than up-down strokes (Fig. 5). Such calls and differences from *S. griseicollis* are discussed further in Krabbe & Schulenberg (2003). Of the other tapaculo species found in the Yariguíes, *S. spillmanni* also gives reeling calls, but of higher frequency (Appendix 3). The calls of an undescribed *Scytalopus* species found at high elevations in the Yariguíes mountains are not dissimilar from *S. g. aburriacantor* trills, but are monotonic (barely varying in acoustic frequency) and of different note shape (no strong up and down strokes). No other *Scytalopus* occurring in the region has a similar voice.

3.2.7 Etymology. This bird is named due to the superficial similarity of its trill to the song of Wattled Guan *Aburria aburri*. The generic (and local) name for that species is combined with the Latin word cantor meaning "singer", to form a non-variable fictional Latin noun *aburriacantor*, declined in the nominative singular.

3.2.8 Taxonomic Rank. The proper modern taxonomic treatment of populations that are phenotypically differentiated but not genetically or vocally diagnosable has been considered recently in the context of both a modern biological species concept (Helbig *et al.* 2002; Remsen 2005) and a modern phylogenetic species concept (Zink 2005). Advocates of both main schools of species concept thought each recommend the recognition of taxa such as *S. g. aburriacantor*. We describe *S. g. aburriacantor* as a subspecies under a modern biological species concept in light of overlap of vocal parameters, following Isler *et al*. (1998).

3.2.9 Ecology. *S. g. aburriacantor* is a skulking bird observed most frequently foraging in dense shrubs of paramo and subparamo ridgetop habitat up to 2 m above ground level. It seems to be most numerous in slightly taller scrub found in sheltered alcoves along exposed ridges and just above the treeline. Stomach contents suggest an insectivorous diet, typical of the genus. The habitat in which

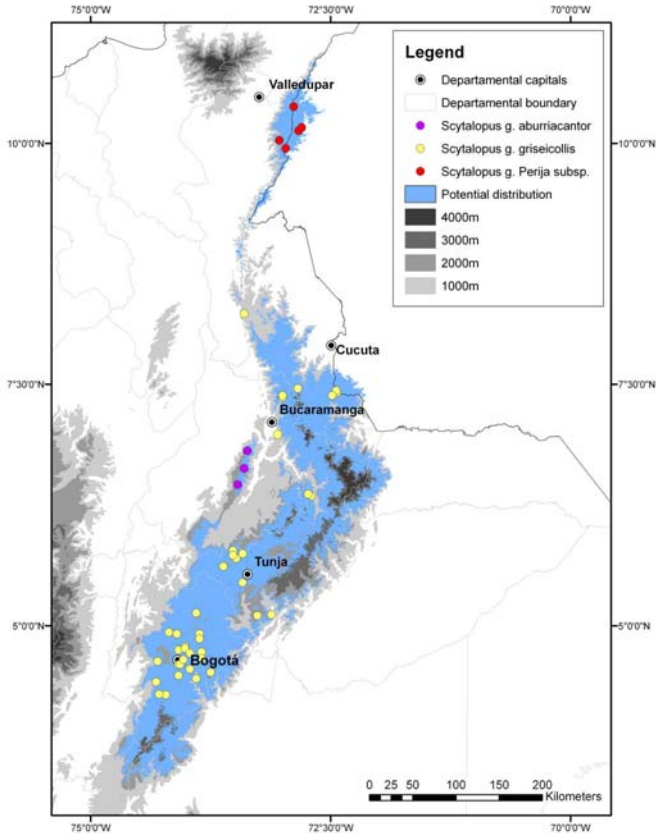
the new subspecies is found is subject to quite extraordinary levels of precipitation and near-constant ground-level cloud (fog). The very humid habitats of *S. g. aburriacantor* may have given rise to a darker population, per "Gloger's rule".

Plants found in *S. g. aburriacantor*'s habitat include Blechnaceae (*Blechnum schomburgkii*), Eriocaulaceae (*Paepalanthus*), Ericaceae, Clusiaceae, Bromeliaceae, Melastomataceae, Orchidaceae, unusual Asteraceae (*Espeletia*) and some isolated tall Palmaceae. At Alto Cantagallos (2450m) on the western slope, *S. g. aburriacantor* was present along an exposed ridgetop only, which presented very stunted vegetation (2m high "canopy") including short, gnarled, winding trees and *Espeletia* of apparently the same species as in the paramo. No individuals were heard calling in the taller and mossier forest below this ridge where *S. latrans* and *S. spillmanni* were present. At Lepipuerto, *S. g. aburriacantor* was heard calling only in the paramo and treeline habitat in small bushes and shrubs. It was not present in mossy montane cloud forest below the treeline, where it was replaced sharply by an undescribed *Scytalopus* species. At this site, calling males of *S. g. aburriacantor* and the undescribed *Scytalopus* were audible within 10 linear metres of one another at the treeline, but never were found together in the same habitat. *S. g. aburriacantor* was common in the paramo of Filo Pamplona, the type locality, but was not present in the montane forest at La Aurora below, though it was heard once from a peculiar primary bamboo forest just below the ecotone, characterised by tall emergent trees, an open canopy with little midstorey and thick bamboo (Poaceae: *Chusquea*) understorey. Below this elevation, it was again replaced by the undescribed species and *S. spillmanni*.

3.2.10 Distribution. We have recorded *S. g. aburriacantor* at high elevations along almost the entire length of Serranía de los Yariguíes in three municipalities (Figure X). However, no skins of the new taxon exist in collections from the main East Andean cordillera.

Our studies of specimens suggests strongly that *S. g. aburriacantor* is an endemic to the highlands of the Yariguíes range. Although *S. griseicollis* was recently sound recorded at 1,300 m in Santander (A. Hernández-J. in litt. 2007), this was in a human-altered habitat. In primary forest, we have not recorded *S. griseicollis* below 2,450 m in Serranía de los Yariguíes or elsewhere. Above 2450m, the Yariguíes massif is isolated from the main Andean cordillera to the south by some 50km by depressions associated with the rivers Opón and Horta. To the north, west and east, the massif is isolated below the 800m contour by arid low elevation valleys of the Magdalena, Sogamoso and Suárez rivers. *S. griseicollis* has been collected and sound recorded at sites very close to this ecological divide in the main East Andes: Arcabuco on the Boyacá /Santander border (*c*.60 km from our Lepipuerto site) and Suratá and Piedecuesta in Santander (*c*.60 km from our Alto Cantagallos site). Cerro de las Armas is the only locality in the intervening region of suitable elevation but has not been surveyed for birds (beyond very brief observations described in Fundación Natura 2003 in which no *Scytalopus* were found).

Figure 7. Map showing localities for nominate *S. g. griseicollis* (yellow circles) and *S. g. aburriacantor* (purple circles) in Eastern Cordillera of Colombia and the Venezuelan border based on museum skins (with thanks to Project Biomap), published recordings and fieldwork by the authors. For reference, localities in Serranía de los Yariguíes are north to south: Alto Cantagallos; Filo Pamplona and Lepipuerto. Coordinates of Yariguíes sites are set out in Appendix 3. Blue highlighting shows the potential range of the species. Note the isolation of the Yariguíes and Perijá populations; and lack of geographic barrier between "*S. infasciatus*" and "*S. griseicollis*" type localities.



3.2.11 Conservation. Serranía de los Yariguíes comprises the largest forest wildernesses in Stattersfield *et al.* (1998)'s East Andes Endemic Bird Area, rated Critical for conservation purposes. The mountain range was for 24 years subject to a "conservation proposal". Following biological justification, including from our studies and others, and the impetus of the Ministerio de Medio Ambiente, Corporación Autónoma Regional de Santander (CAS), CDMB, various mayoralties of the region and NGOs, the Serranía de los Yariguíes National Park was finally declared on 16 May 2005 (Ministerio del Medio Ambiente, Desarrollo y Vivienda 2005). NGOs have declared the region an Alliance for Zero Extinction site (Ricketts *et al.* 2005) and an Important Bird Area (AICA) (Franco & Bravo 2005) and Fundación ProAves has established a nature reserve in the region (discussed

further in Donegan & Huertas 2005; Huertas & Donegan 2006). These new protected areas should help protect the natural habitat of *S. griseicollis aburriacantor* and other threatened birds including White-mantled Barbet *Capito hypoleuca*, Chestnut-bellied Hummingbird *Amazilia castaneiventris*, Black Inca *Coeligena prunellei*, Gorgeted Wood-Quail *Odontophorus strophium*, Mountain Grackle *Macroagelaius subalaris*, Rusty-faced Parrot *Hapalopsittaca amazonina* and Saffron-headed Parrot *Gyopsitta pyrilia* (Donegan & Briceño 2005; Donegan & Avendaño-C. 2006).

Although bird conservation assessments often consider only species level taxa (e.g. BirdLife International 2004), distinctive subspecies are of conservation relevance (e.g. Peterson & Navarra 1999; Zink 2003; Cadena 2003). An assessment of the new taxon's conservation status therefore follows below.

The area of occurrence of *S. g. aburriacantor* is rather difficult to determine because the taxon is principally present (and abundant) in the ecotone between paramo and forest which does not correspond to any elevational band but rather varies in width and elevation with topography and on different slopes. *S. g. aburriacantor* is present neither in the more windswept paramo of very high elevations (which consists principally of stunted bromeliads and reeds) nor in forest below the treeline.

Based on fieldwork, we estimate that suitable ecotone habitats occupy an average latitudinal width of *c.*100m on the west slope and *c.*200m on the east slope (the latter including a broader habitat transition). On the west slope, approximately 51km of the massif occurs at suitable elevations for the species (*c.*2500-3000m), whilst on the east slope, 25 km attains suitable elevations (3100-3200m) (IGAC 1995). In both regions, the massif is forested (IGAC 1999). The figures above would produce an estimated area of suitable habitat of 12.6km^2 (5.1km^2 for the west slope and 7.5km^2 for the east slope). *S. g. aburriacantor* is abundant in such

habitats. In the three patches of suitable habitat that we have studied: at least 5 calling males were present in a 250 x 200m area at Pamplona; at least 1 male was present in a 80 x 3 m area along a ridge at Cantagallos; and at least 1 in a 50 x 50m area at the ecotone in Lepipuerto. For each male, a female is assumed present. 14 individuals in 5.27ha produces an average density of 2.65 individuals/ha or 265 individuals/km^2. Assuming 70-100% occupancy in suitable habitat produces a total estimated population of around 2310-3340 individuals. Despite its small range, *S. g. aburriacantor* would not qualify for Vulnerable under category D1 on a basis of its population alone, but could be considered Near-Threatened. We have insufficient data to know if it would qualify under other categories, but the relative intactness of the remaining forest at high elevations suggests that the population is unlikely to be declining by >30% over ten years (criterion A), nor that the habitat is "severely fragmented" (necessary for this species to trigger criterion B). Deforestation continues in lowlands and foothill to premontane regions of the Yariguíes mountains, but the highest elevations remain remote. Given the inaccessibility of *S. g. aburriacantor*'s habitat, its high abundance where found, lack of hunting or bird trade threats for *Scytalopus*, the adaptability of *S. griseicollis* to secondary habitats generally and the protected status of the Yariguíes mountains, we are not particularly concerned for the long-term conservation of this bird taxon at present. *S. g. aburriacantor* may, however, be threatened in future by range expansions of the nominate subspecies with deforestation as *S. g. griseicollis*' adaptability to lower elevation secondary habitats would make it capable of expanding in range to the depressions currently isolating the Yariguíes massif from the rest of the East Andes.

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Appendix 1: Specimens examined

All specimens localities are in Colombia unless otherwise stated.

Myornis senilis: BMNH 86.6.24.515, 86.6.24.516, 89.9.20.687, 89.9.20.688, 89.9-10.972, 89.9-10.974 (all "Bogotá"), 1916.8.24.58 (Baeya, E. Ecuador), 1916.8.24.60, 1916.8.24.69 (both, "E. Ecuador"), 1940.12.5.1005, 1940.12.5.1006 (both, Volcan Pichincha, Ecuador); ICN 12002-12006 (all, San Miguel, Cundinamarca), 26257 (Paez, PNN Nevado del Huila, Cauca), 35024, 35027 (both, Frontino, Urrao, Antioquia); MLS 3984 (PNN Chingaza, Boyacá), 3986 (San Miguel, Sibate, Cundinamarca).

Scytalopus latrans: BMNH 89.9.20.684 to 89.9.20.686 (all, Santa Elena, Antioquia), 89.9.20.702, 89.7-10.969, 89.7-10.970 (all Santa Elena or Medellín, Antioquia), 89.7-10.970 ("Colombia") 89.7-10.972 ("Bogota"), 1916.8.24.61, 1921.12.29.179 to 1921.12.29.181 (all, Munchique or Popayán, Cauca), 1940.12.5.1014 to 1940.12.5.1016 (all, Ecuador); COP (all Venezuela) 9088 and 9382 (both, Queniquea, Táchira, 1900m and 1600m), 10911 (Páramo de Tamá, Villa Paez, Táchira, 2200m), 24554 (Boca de Monte; Pregonero, Táchira, 1950-2000m), 61231 to 61234, 62232 to 62235, 62238 to 62243 (Río Chiquito, Hacienda La Providencia, Táchira, 1800-2250m); IAVH 2476 (Cauca), 6723 (Quebrada Bomobona, Finca Indostán, Anzoategui, Tolima), 8220 (Santa Leticia, km 129, Cauca), 8221 (San Rafael, PNN Puracé, Cauca), 10257 (PNN Los Picachos, San Vicente del Cagüán, Caquetá), 10654 (Sector Orocué, PNN Tamá, Herrán, Norte de Santander), 11682 (Bojacá, Cundinamarca); ICN 3500 (Alto de Ventanas, Jardín, Antioquia, 2900m), 4763 to 4767, 4846, 11992, 11998, 11999, 12000, 12968 (all, Aguabonita, Silvania, Cundinamarca), 11989, 11990, 11993 to 11997, 11999 (all, San Miguel, Cundinamarca, 2800m), 22186 (vereda Farralorado, Choachí, Cundinamarca, 2300m), 25906, 26032, 26048, 26074 (all, Corea, PNN Farallones de Cali, Valle del Cauca), 30933, 30934 (both, 3km NE of Monterredondo, Camino a

San Juanito, Guayabetal, Cundinamarca, 2050m), 31788 (Cuchillas de Santa Barbara, Bojacá, Cundinamarca, 2600m), 33460, 33477 (both, Torre Telecom, Serranía de los Churumbelos, Cauca, 2400m), 34704 (El Escobero, San Sebastian, Retiro, Antioquia), 35023 (Frontino, Urrao, Antioquia, 3159m), 36177 (El Talisman, Serranía de los Yariguíes, Santander, 2100m); MLS 2977 (Alturas de Medellín, Antioquia), 3978 to 3981, 3983 (all, Pamplona, Norte de Santander), 3982 (Tequendama, Cundinamarca), 4798 (Yarumal, Antioquia), 8070 (Boquerón, Medellín, Antioquia), 8583 (Medellín, Antioquia); MNHN 522, 523, 1334, 1996 (all, "Ecuador"), 1336 (Pichincha, Ecuador), 1387 (Cerro Majanda, Ecuador), 2003.885 ("Colombia").

S. undescribed species: ICN 35607 (La Aurora, Galán, Serranía de los Yariguíes, 2750m; sound recording).

S. micropterus: BMNH 89.9-10.983 ("Ecuador"), 1940.12.5.343 (Cututucu, Macas, Ecuador), 1953.68.679 (Soldados Range, Azuay, Ecuador), 1953.68.879 (Macuina, Ecuador); ICN 33263, 33267 (both, Villa Iguana, Serranía de los Churumbelos, Cauca); MNHN 1391 (E. Ecuador), 1933 (Alucincho, Ecuador).

S. atratus (includes specimens labelled "*confusus*" and "*nigricans*"): BMNH 89.9.20.699 ("Bogotá"); COP (all Venezuelan) 54928 and 54929 (Sierra de Perijá, Cerro Pejochaina, Falda Oeste, Zulia, 1900-1950m), 61224 to 62237 (Río Chiquito, Hacienda La Providencia, Táchira, 1800-1900m), 60640A to 60640L (Burguam, Cumbre, Cerro El Teteo, Táchira, 1200-1300m); ICN 32621 (vereda Aguas Claras, Serrania de Aguas Claras, Cubarral, Meta), 34387 (Anorí, Antioquia), 35613 (Alto Honduras, Serranía de los Yariguíes, Santander, 1600m; sound recording); MNHN 386 (no data).

S. panamensis: BMNH 1921.7.3.69 (Tacarcuna, Panama).

S. rodriguezi: BMNH 1921.12.29.190 (La Palma, Huila); ICN 34845, 35234 (both, Finca Merenberg, Huila).

S. rodriguezi undescribed subspecies or related but undescribed species: BMNH 89.9-10.995 ("Bogotá"); ICN 35821 (La Luchata, Galán, Serranía de los Yariguíes, 2000m) 36178, 36179 (both, El Talisman, San Vicente de Chucurí,

Serranía de los Yariguíes, 2100m; sound recording); MLS 3990 to 3993 (all Fontibon or Alturas de Pamplona, Norte de Santander).

S. undescribed species? (all Venezuela): COP 14363 (El Valle, Mérida, 2200m), 62230 (Río Chiquito, Hacienda La Providencia, Táchira, 2180-2250m), 65395 and 65396 (La Azulita, Mérida, 2300m).

S. stilesi: ICN 34420, 34505, 34512, 34615, 34584, 34609, 34610 (all, Amalfí, Antioquia).

S. vicinior: ICN 31207, 31208 (both, 8km NE of Jeguadas, Alto de Pisones, Mistrata, Risaralda), 34840 (finca La Minga, vereda Chicoral, Cato Bitaco, La Cumbre, Valle).

S. latebricola: ICN 23338 (San Lorenzo, Santa Marta, Magdalena).

S. meridanus (all Venezuela): AMNH 492377 (La Culata, Mérida, 4000m: type); COP 9441 (Páramo Zumbador, Táchira, 2600m), 14205 to 14208 (all, Llano Rucio, Mérida, 2500m), 14523 (Quintero, Mérida, 2800m), 14577 (El Escorial, Mérida, 2800m), 20177 to 20181 (all, Cerro Niquitaz, El Rincón, Trujillo, 2200-2300m), 24547 to 24553 (all Boca de Monte, Pregonero, Táchira, 1950-2400m), 26240 (Guamito, Trujillo), 45378 to 45384 (all, Páramo Aricagua, El Muerto, Falda Norte, Merida, 3000-3140m), 49294 to 49298 (Santo Domingo, Mérida, 2300-2700m), 62227 to 62229, 62231, 62244, 62245 (Río Chiquito, Hacienda La Providencia, Táchira, 2180-2300m), 64259 to 64272 (Páramo La Negra, Mérida, 3200-3250m), 65206 (Guaraque, Mérida, 2250m or 1600m), 65312 (La Montaña Teleférico, Mérida, 2600-2650m), 65394 (La Azulita, Mérida, 2300m), 65397 (La Azulita, Mérida, 2100m), 71525 (35 km S of Mucuchíes, Barinas, 2500m), 73946 to 73952 (La Revancha, Cumbre, Cerro El Retiro, Táchira, 2700-2800m); MNHN 523, 599 (both, Mérida). Specimens labelled *"S. fuscicauda"*: BMNH 89.9.20.695 (Mérida), 89.9-10.999 (Sierra Nevada, Mérida), 1914.11.26.506 (Mérida), 1914.11.26.507 (La Culata, Mérida, 3000 m), 1914.11.26.505 (Mérida); COP 19963 to 19967 (all Páramo de Cendú, Cendú, Trujillo, 2700-2960m), 26240 (Guamito, Trujillo).

S. caracae: (all Venezuela) BMNH 47.7.16.12 (“Caracas”); COP 226, 13047 to 13051, 56781 to 56787, 58459 to 58472, 61644 to 61648 (all, El Junquito, Distrito Federal, 1900-1950m), 1469 to 1470, 13384 to 13384 (all, Colonia Tovar, Aragua, 1900-1950m), 3345 to 3346 (all, Cerro El Avila; Plan de Los Lirios, San Isidrio, Distrito Federal, 1600-1700m), 13152 to 13155, 58455 to 58458, 61642 to 61643 (Caracas, León, Distrito Federal, 2000-2100m), 18850 to 18852 (all, Guarenas, Hacienda Izcaragua, Miranda, 1400-1880m), 62603 to 62614 (all, Cerro el Avila, San Isidro, Distrito Federal, 2000m), 62615 to 62617 (both, Cerro el Avila, San Antonio de Galipán, Distrito Federal, 1600m), 62618 (Cerro el Avila, Estación Telefórico, Distrito Federal, 2100m), 62619 to 62621 (Cerro el Avila, Cerro Papelón, Distrito Federal, 1850-1900m), 75775 and 78732 (both, Colonia Tovar; Fundo Jeremba, Aragua, 2300m).

S. spillmanni: BMNH 1902.3.13.1261 (Porvenir, Bolivar, Ecuador), 1921.12.29.189 (La Guneta, Quindio, 10,300ft.); ICN 35026, 35029 (both, Paramo Frontino, Antioquia, 2600m), 35032-35034 (all, vereda Meseria, Jardín, Antioquia, 2300m), 33166 (Ucumari, Risaralda); MfN 1937.11.76 (type: Volcán Iliniza, Pichincha / Cotopaxi, Ecuador).

S. spillmanni undescribed subspecies: ICN 35605, 35608 (both, La Aurora, Galán, Serranía de los Yariguíes, Santander; sound recording).

S. g. griseicollis (including specimens labelled "*S. infasciatus*"): AMNH 132328 (type of *S. infasciatus*: Páramo de Beltrán); BMNH 44.12.31.16, 44.12.31.24, 69.8.16.31, 80.4.30.33, 80.4.30.34, 89.9.20.691 to 89.9.20.694, 89.9-10.978, 89.9-10.996, 89.9-10.999 (all “Bogota”), 2002.3.1014 (“New Grenada”); COP 11101 to 11103 (all, PNN Tamá, Apure, Venezuela 2800m); IAVH 10305 (Mamaramos, SFF Iguaque, Boyacá), 12282 (vereda Ermitaño, Sutamarchán, Boyacá), 12586 (vereda La Capilla, near SFF Igüaque, Villa de Leyva, Boyacá), 12701, 12712, 12716, 12717, 12720 (all, vereda San Francisco, Guasca, PNN Chingaza, Cundinamarca), IAVH 10625, 10664, 10728 (all, Sector Orocué, Herrán, PNN Tamá, Norte de Santander), 12068, 12123, 12125 (all, vereda Carrizal, Sector Sisavita, Cucutilla, Norte de Santander); ICN

10852 (vereda Ruparita, 2km E of Arcabuco, Boyacá), 10853 (vda Puente Boyacá, Ventaquemala, Boyacá), 11982 to 11984 (all, Paramo de Guasca, Cundinamarca, 3500m), 11985 to 11988 (all, Alto Onzaga, Soatá, Boyacá), 12001 (Guasca, Cundinamarca), 12007 (La Mercedes, km 25, Carretera La Herrera - La Mesa, Cundinamarca), 12008 to 12009 (Boquerón de Chipaque, Cundinamarca), 12010 (Laguna de Chisacal, Cundinamarca, 3900m), 12011 to 12012 (Choachí, Cundinamarca), 12013 (Subachoque, Cundinamarca), 12014 to 12016 (both, Paramo de Guasca, Cundinamarca) 13015 to 13017 (Paramo de Palacio, Cundinamarca), 14074 (hacienda El Otoño, Sabana de Bogotá, Cundinamarca), 19963 (Montserrate, Bogotá, Cundinamarca), 24920 (Boqueron de Juan Viejo, Pasca, Cundinamarca), 31235, 31236 (both, Paramo de Chingaza, Piedras Gordas, La Calera, Cundinamarca), 31798 (Suba, Cerro La Conejera, Bogotá, Cundinamarca), 34492 (Bosque de Torca, cerros orientales de Bogotá, Cundinamarca, 3050m), 34780 (vereda Aurora, altos cerros orientales, Bogotá, Cundinamarca), 35441 (vereda Molinos, Soatá, Boyacá), 36121 (Suratá, Santander), (unnumebred (Piedecuesta, Santander); MLS 3985 (Nomocón, Cundinamarca), 3988 (Tabio, Cundinamarca), 3989 (La Calera, Cundinamarca); MCZ 76330, 76331 (both, types of *S. griseicollis*: “Bogotá”); MNHN 518, 2001.519, 2003-894 (all, “Colombia”).

S. griseicollis subspecies from Perijá: COP (all Venezuela) 54930 to 54933, 54945 to 54947 (all, Sierra de Perijá, Cerro Pejochaina, Cumbre, Zulia, 1900-2350m), 54934 to 54944, 54948 (all, Sierra de Perijá, SE Cerro Tetari, Zulia, 2900m), 57708 (all, Sierra de Perijá, Pie Nudo 4 de Febrero, Zulia, 2600m), 57709 to 57710 (all, Sierra de Perijá, Fila Macoita, Campamento Avispa, Zulia, 2175m), 72846 to 72855 (all, Sierra de Perija, Frontera, Zulia, 2750-3050m), 74170 to 74172 (all, Sierra de Perijá, Cerro Viruela, Zulia, 3100m); ICN 36125 and 36126 (both vereda El Cinco, Mauaure, Serranía de Perijá, Cesar, Colombia, 2600m).

S. g. aburriacantor: ICN 35609, 35610, 36175 (details of each in text above).

S. canus canus: BMNH 1921.7.3.70 (Paramillo, Antioquia, 12,500 ft); ICN 35020 (Paramo Frontino, Urrao, Antioquia, 3500m).

S. canus opacus: BMNH 1953.68.680 (Pichincha, Ecuador); MNHN 1390 (Cerro Mojanda, Ecuador).

Appendix 2: biometrics of northern Rhinocryptidae

In the below table, all data is from Colombia and Venezuela, with species marked * also including data from NHM and MNMH specimens from Ecuador. For each species' measurement, data is presented as follows: mean ± standard deviation (n= sample number). Species order and nomenclature generally follows Remsen *et al*. (2006), as modified herein.

Taxon	**Wing chord from skins (mm)**	**Tail (mm)**	**Tarsus (mm)**	**Full culmen (mm)**	**Body mass (g)**
*Myornis senilis** [1]	56.7 ± 1.9 (n=19) (54.0-61.0)	58.6 ± 4.4 (n=20) (53.0-63.0)	22.0 ± 0.4 (n=19) (21.5-23.0)	15.7 ± 0.7 (n=19) (14.5-17.0)	19.0 ± 0.7 (n=2) (18.5-19.5)
M. senilis W Andes	56.0 ± 0.0 (n=2) (56.0-56.0)	68.5 ± 0.7 (n=2) (68.0-69.0)	22.0 ± 0.0 (n=2) (22.0-22.0)	16.8 ± 0.4 (n=2) (16.5-17.0)	19.0 ± 0.7 (n=2) (18.5-19.5)
M. senilis C Andes*	58.2 ± 2.4 (n=5) (55.0-61.0)	58.3 ± 2.4 (n=6) (56.0-62.0)	22.0 ± 0.0 (n=6) (22.0-22.0)	16.2 ± 0.3 (n=5) (16.0-16.5)	/
M. senilis E Andes	56.3 ± 1.7 (n=12) (54.0-60.0)	57.1 ± 3.3 (n=12) (53.0-63.0)	22.0 ± 0.6 (n=11) (21.5-23.0)	15.4 ± 0.6 (n=16) (14.5-16.5)	/
*Scytalopus latrans**	56.0 ± 2.7 (n=48) (52.0-60.0)	39.6 ± 2.2 (n=43) (35.0-43.0)	22.5 ± 0.9 (n=47) (21.0-24.0)	13.6 ± 0.9 (n=45) (12.0-14.5)	18.1 ± 1.7 (n=12) (16.0-21.0)

S. latrans W Andes	54.0 ± 2.2 (n=4) (52.0-57.0)	39.3 ± 1.7 (n=4) (37.0-41.0)	22.3 ± 0.5 (n=4) (22.0-23.0)	12.8 ± 1.1 (n=2) (12.0-13.5)	/
S. latrans C Andes [2]	57.5 ± 2.5 (n=9) (53.0-60.0)	38.6 ± 2.0 (n=9) (36.0-41.5)	22.7 ± 0.9 (n=10) (21.0-24.0)	13.7 ± 0.6 (n=10) (12.0-14.5)	19.4 ± 1.5 (n=3) (18.0-21.0)
S. latrans E Andes	55.0 ± 2.1 (n=28) (52.0-60.0)	39.7 ± 2.2 (n=25) (36.0-43.0)	22.4 ± 0.9 (n=27) (21.0-24.0)	13.4 ± 0.6 (n=27) (12.0-14.5)	17.4 ± 1.7 (n=7) (16.0-19.3)
S. sp. (Pied-billed)	52 (n=1)	35 (n=1)	21.5 (n=1)	14.0 (n=1)	18.7 (n=1)
*S. micropterus**	59.2 ± 2.9 (n=6) (55.0-61.0)	49.6 ± 4.8 (n=5) (44.0-56.0)	24.5 ± 1.1 (n=5) (23.0-26.0)	16.0 ± 0.7 (n=4) (15.0-16.5)	/
S. atratus (nominate and *S. a. confusus*)	57.0 ± 1.4 (n=6) (55.0-59.0)	40.0 ± 2.6 (n=6) (36.0-43.0)	22.5 ± 0.9 (n=6) (21.0-23.5)	14.6 ± 0.6 (n=6) (14.0-15.5)	/
S. panamensis	51 (n=1)	39 (n=1)	/	14.5 (n=1)	/
S. rodriguezi	54.3 ± 2.1 (n=3) (52.0-56.0)	47.0 ± 1.7 (n=3) (45.0-48.0)	22.5 ± 0.9 (n=3) (22.0-23.5)	14.8 ± 0.3 (n=3) (14.5-15.0)	21.5 ± 0.1 (n-2) (21.4-21.6)
S.rodriguezi sp. (E. Andes: Col.)	57.0 ± 2.3 (n=7) (53.0-60.0)	37.5 ± 2.2 (n=7) (34.0-40.2)	21.8 ± 0.9 (n=6) (20.5-23.0)	13.1 ± 1.3 (n=7) (11.5-15.0)	17.4 ± 0.6 (n=3) (16.7-18.0)
S. sp.	53.0 ± 1.8	42.7 ± 0.6	22.4 ± 0.9	13.3 ± 0.3	/

(Ven. Andes)	(n=4) (51.0-54.0)	(n=3) (42.0-43.0)	(n=4) (21.5-23.5)	(n=3) (13.0-13.5)	
S. stilesi	56.5 ± 0.8 (n=6) (55.0-57.0)	43.3 ± 1.4 (n=6) (41.0-45.0)	22.8 ± 0.6 (n=7) (22.5-24.0)	15.1 ± 0.5 (n=6) (14.5-16.0)	21.3 ± 0.8 (n=6) (20.0-22.0)
S. vicinior	57.0 ± 1.7 (n=3) (56.0-59.0)	46.0 ± 2.6 (n=3) (43.0-48.0)	22.7 ± 0.8 (n=3) (22.0-23.5)	14.7 ± 0.3 (n=3) (14.5-15.0)	24.2 ± 2.6 (n=3) (21.5-26.7)
S. latebricola	58 (n=1)	36 (n=1)	23.0 (n=1)	14.0 (n=1)	/
S. caracae	52.8 ± 1.6 (n=5) (50.0-54.0)	39.8 ± 1.9 (n=5) (37.0-42.0)	21.9 ± 0.7 (n=5) (21.0-23.0)	14.5 ± 0.5 (n=5) (14.0-15.0)	/
*S. spillmanni** (all)	58.9 ± 2.5 (n=10) (56.0-65.0)	42.1 ± 2.7 (n=9) (39.0-47.0)	23.6 ± 1.0 (n=9) (22.0-25.0)	14.6 ± 0.7 (n=10) (13.5-15.5)	23.7 ± 2.3 (n=8) (22.0-27.0)
S. griseicollis (including *"S. infasciatus"*; excluding Tamá & Perijá)	54.7 ± 2.6 (n=42) (50.0-61.0)	39.8 ± 1.9 (n=29) (36.5-43.5)	21.9 ± 0.9 (n=44) (20.0-23.5)	12.7 ± 0.7 (n=39) (11.0-14.0)	17.1 ± 2.5 (n=13) (11.0-21.0)
S. griseicollis Males	55.2 ± 2.7 (n=24) (52.0-61.0)	34.0 ± 1.6 (n=16) (38.0-43.5)	22.2 ± 1.0 (n=23) (20.0-23.5)	12.9 ± 0.7 (n=39) (11.0-14.0)	17.3 ± 2.8 (n=9) (11.0-21.0)
S. griseicollis Females	54.8 ± 2.5 (n=9) (50.0-59.0)	38.7 ± 1.8 (n=7) (36.5-41.0)	21.5 ± 0.7 (n=8) (20.5-22.5)	12.3 ± 0.7 (n=8) (11.5-13.0)	16.5 ± 1.9 (n=4) (16.0-18.0)

S. griseicollis aburriacantor Males	57.0 ± 1.0 (n=3) (56.0-58.0)	44.3 ± 0.6 (n=3) (44.0-45.0)	22.5 ± 0.5 (n=3) (22.0-23.0)	13.6 ± 0.4 (n=3) (13.0-14.0)	17.8 ± 0.4 (n=2) (17.5-18.0)
S. griseicollis (Tamá)	55.9 ± 2.8 (n=9) (52.0-60.0)	41.0 ± 2.5 (n=9) (36.5-44.0)	21.5 ± 0.8 (n=9) (20.5-22.5)	12.8 ± 0.5 (n=8) (12.0-13.5)	16.3 ± 0.8 (n=5) (15.0-17.0)
S. griseicollis (Tamá) Males	57.5 ± 1.9 (n=4) (56.0-60.0)	41.3 ± 2.9 (n=4) (38.5-44.0)	22.1 ± 0.6 (n=4) (21.5-22.5)	12.9 ± 0.6 (n=4) (12.0-13.5)	17.0 ± 0.0 (n=2) (17.0-17.0)
S. griseicollis (Tamá) Females	54.6 ± 2.8 (n=5) (52.0-58.0)	40.7 ± 2.5 (n=5) (36.5-43.5)	21.0 ± 0.5 (n=5) (20.5-22.0)	12.7 ± 0.4 (n=4) (12.0-13.0)	15.8 ± 0.8 (n=3) (15.0-16.0)
S. griseicollis (Perijá)	51.9 ± 2.5 (n=28) (48.0-55.0)	38.5 ± 1.5 (n=26) (36.0-42.5)	21.1 ± 1.0 (n=27) (18.5-22.5)	14.0 ± 0.6 (n=22) (13.0-15.5)	/
S. griseicollis (Perijá) Males	52.7 ± 2.6 (n=11) (49.0-55.0)	39.4 ± 1.7 (n=10) (37.0-42.5)	21.6 ± 0.9 (n=11) (19.5-22.5)	14.3 ± 0.5 (n=10) (13.5-15.5)	/
S. griseicollis (Perijá) Females	51.9 ± 2.3 (n=12) (48.0-54.0)	38.3 ± 1.2 (n=11) (37.0-40.0)	20.9 ± 0.9 (n=12) (19.5-22.5)	13.8 ± 0.5 (n=9) (13.0-14.5)	/
S. meridanus (inc. "*S. fuscicauda*")	50.8 ± 2.2 (n=45) (46.0-55.0)	38.4 ± 2.2 (n=37) (34.0-43.0)	21.3 ± 0.9 (n=45) (20.0-23.0)	13.0 ± 0.6 (n=42) (12.0-14.0)	/
S. meridanus Males	50.9 ± 2.5 (n=8) (48.0-54.0)	40.2 ± 1.9 (n=6) (38.0-43.0)	21.5 ± 0.8 (n=8) (20.5-23.0)	13.4 ± 0.6 (n=8) (12.5-4.0)	/

S. meridanus Females	50.1 ± 2.3 (n=22) (44.0-53.0)	37.3 ± 2.0 (n=16) (34.0-43.0)	20.9 ± 0.7 (n=22) (19.5-22.5)	12.9 ± 0.7 (n=20) (12.0-14.0)	/
S. canus canus	49.0 ± 2.9 (n=2) (47.0-51.0)	34.0 ± 1.4 (n=2) (33.0-35.0)	21.5 ± 0.7 (n=2) (21.0-22.0)	12.5 ± 0.7 (n=2) (12.0-13.0)	/
S. canus opacus	50.5 ± 2.1 (n=2) (49.0-52.0)	36.5 ± 0.7 (n=2) (36.0-37.0)	20.8 ± 1.1 (n=2) (20.0-21.5)	11.8 ± 0.4 (n=2) (11.5-12.0)	/

Footnotes:

[1] Adult specimens from Ecuador appear somewhat darker than those from the East Andes of Colombia. Juveniles also show further differences, with East Andes specimens often having a rufous wing flash, a feature we have not observed in skins of *M. senilis* juveniles from Ecuador nor noted in Ridgely & Greenfield (2001) or Krabbe & Schulenberg (1997, 2003). Variation in darkness of plumage and biometrics is also evident between populations of Colombia's three Andean cordilleras. It seems possible that various taxa and/or some clinal variation may be involved.

[2] *S. latrans* specimens from the northern Central Andes are greyer than both West Andes and East Andes birds, although the song is similar in both the Central and East Andes. Krabbe & Schulenberg (1997) also reported differences in plumage darkness between west and east slope populations of this species in Ecuador.

Appendix 3: Vocal parameters of calls of nominate *S. griseicollis* and *S. g. aburriacantor*

For each species and call, data is presented as follows: mean ± standard deviation (lower bound of data - upper bound of data). Gazzetteer of recording localities: *S. g. aburriacantor*: Alto Cantagallos, mun. San Vicente de Chucurí, Serranía de los Yariguíes, Santander, Colombia (06°49'N; 73°22'W; 2450m) (TMD recordings); Lepipuerto, mun. El Carmen / Zapatoca, Serranía de los Yariguíes, Santander, Colombia (6°28'N; 73°28'W; 2900m) (TMD recordings); Filo Pamplona, Mun. Galán, Serranía de los Yariguíes, Santander, Colombia (06º38'N; 73º24'W; 3200m) (TMD & JEAC recordings). *S. g. griseicollis*: Tamá, Río Oría, Apure state, Venezuela (C. Parrish recoring: xeno-canto 6079); Suratá, Santander (07°23'N; 73°00W; 3000m) (JEAC recordings); Rogitama, mun. Arcabuco, Boyacá, Colombia (05°47'N, 73°31'W; 2500m) (J. Zuluaga, R. Chavarra & J. Beckers recordings); Soatá, Boyacá, Colombia (05°07'N, 73°07'W; East Andes) (O. Cortés, A. Hernández & O. Laverde recordings); SFF Iguaque, Boyacá, Colombia (Sector Carrizal) (05º44'N; 73º31'W; 2800 m) (J. Zuluaga recordings); Reserva Privada el Secreto, Vereda Cienaga-Valvanerra, mun. Garagoa, Boyacá, Colombia, 2000-2200 m (O. Laverde recordings); finca San Cayetano, vereda Fute, mun. Bojacá, Cundinamarca, Colombia (4º38'N, 74º18' W, 2650 m) Fute (O. Laverde recording); PNN Chingaza, Cundinamarca, Colombia (J. Parra & O. Laverde recordings); Monserrate, Bogotá, Cundinamarca, Colombia (J. Beckers recordings); Quebrada La Vieja, Bogotá, Colombia, 2900 m (D. Knapp recording: xeno-canto no. 10866); finca La Carbonera, vereda el Roble, inspección La Aguadita, mun. Fusagasugá, Cundinamarca, Colombia (4°25'N, 74°19'W, 2450-2550 m) (O. Laverde recordings). *S. meridanus*: 10 km SE of La Azulita, Mérida, Venezuela, 2300m (C. Parrish & A. Spencer recordings: xeno-canto nos. 6234, 6235, 6236, 14790); Pico Humboldt Trail, Parque Nacional Sierra Nevada, Mérida, Venezuela, 2500m (N. Athanas & A. Spencer recordings: xeno-canto 8249 and 11243); Paramo de Zumbador, Táchira, Venezuela (2500-2700m) (B10_2C.WAV in Boesman 1999);

Yacumbu NP, Lara, Venezuela (1700m) (A09A_2C.WAV in Boesman 1999); Laguna Mucubaji area, Merida, Venezuela (3200m) (B10A_2C.WAV in Boesman 1999); Paramo de Batallón, Táchira, Venezuela (2700-2900m) (A17A_2C.WAV in Boesman 1999); Humucaro Alto, Lara, Venezuela (2650m) (A33B_2C.WAV in Boesman 1999); Guaramacal NP, Trujillo, Venezuela (2400-2600m) (B19A_2C.WAV, B21A_2C.WAV and B27A_2C.WAV in Boesman 1999). *S. spillmanni*: La Aurora, finca Pamplona, Serranía de los Yariguíes, vereda San Isidrio, municipio Galán, Santander Dept, Colombia (06º 38' N; 73º 24' W; 2700 m) (T. Donegan & J. Avendaño recordings), Finca La Carbonera, Los Robles, La Aguadita, Fusagasugá, Cundinamarca (4°25'N, 74°19'W, 2450-2550m) (O. Laverde recording).

Call type / *Taxon*	**No. of calls / no. of recordings: overall and by locality.**	**Length of call (s)**	**No. of notes in call**	**Notes/s**	**Max. frequency of first overtone in lowest note (kHz)**	**Max. frequency of first overtone in highest note (kHz)**
			Trill			
S. g. griseicollis	164/22: Tamá (9/1), Rogitama (38/5), Chingaza (92/11); Soatá (4/2), Garagoa (7/1), Suratá (3/1), Bojacá (8/1), Fusagasugá (2/1) and Montserrate (1/1).	1.13 ± 0.35 (0.35-2.00)	30.31 ± 10.06 (8.00-52.00)	27.84 ± 2.33 (21.62-32.31)	2.92 ± 0.28 (2.20-3.70)	3.76 ± 0.28 (3.00-4.20)
S. g.	75/13: Alto	1.11 ± 0.17	31.36 ±	28.10 ± 2.64	2.39 ±	3.20 ± 0.26

aburriacantor	Cantagallos (19/3), Lepipuerto (30/7) and Filo Pamplona (26/4).	(0.70-1.50)	4.94 (21.00-43.00)	(21.82-33.64)	0.31 (1.70-2.90)	(2.60-3.60)
S. meridanus	14/3: Páramo de Batallón (7/1), Guaramacal NP (6/1) and La Azulita (1/1).	1.16 ± 0.30 (0.75-1.60)	21.14 ± 6.47 (12.00-31.00)	18.06 ± 1.04 (16.00-19.23)	4.96 ± 0.23 (4.70-5.30)	5.44 ± 0.20 (5.20-5.70)
Reeling Call						
S. g. griseicollis	48/16: Suratá (3/1), Chingaza (23/9), Iguaque (4/1), Soatá (3/1), Fusagasugá (6/1) Monserrate (2/1), La Vieja (4/1) and Rogitama (3/1).	2.53 ± 3.47 (0.15-13.35)	61.19 ± 79.96 (4.00-293.00)	25.93 ± 3.08 (21.00-32.00)	2.48 ± 0.18 (2.20-2.90)	2.81 ± 0.18 (2.50-3.20)
S. g. aburriacantor	6/3: Lepipuerto (3/1) and Filo Pamplona (3/2).	1.08 ± 0.57 (0.65-2.00)	31.33 ± 16.92 (19.00-60.00)	28.89 ± 0.87 (27.50-30.00)	2.84 ± 0.13 (2.70-3.00)	2.95 ± 0.23 (2.70-3.30)
S. meridanus	10/7: La Aazulita (1/1), Pico Humboldt (2/2), Paramo de Zumbador (1/1) Yacumbu NP (4/1), Guaramacal NP (1/1), Mucubaji (1/1) and Humucaro Alto	15.46 ± 8.00 (7.80-31.90)	214.86 ± 117.72 (68.00-479.00)	14.10 ± 3.60 (8.50-19.80)	3.38 ± 0.24 (3.00-3.90)	3.96 ± 0.23 (3.60-4.40)

	(1/1).					
S. spillmanni subsp. (East Andes)	32/10: Yariguíes (16/9) and Fusagasuga (16/1).	3.35 ± 3.84 (0.60-13.50)	80.70 ± 101.16 (20.00-392.00)	29.49 ± 1.68 (25.33-32.25)	3.14 ± 0.16 (2.90-3.60)	3.75 ± 0.15 (3.50-4.10)
Churr						
S. g. griseicollis	92/9: Bogotá (1/1), Chingaza (42/3), Suratá (26/2), Iguaque (5/1) & Soatá (18/2).	1.63 ± 0.42 (0.65-2.00)	43.17 ± 10.19 (15.00-47.00)	23.16 ± 1.83 (20.00-26.96)	2.66 ± 0.25 (1.70-2.50)	3.32 ± 0.20 (2.50-3.40)
S. g. aburriacantor	33/8: Lepipuerto (32/7) and Filo Pamplona (1/1).	1.14 ± 0.23 (0.90-1.80)	23.69 ± 4.52 (18.00-37.00)	21.35 ± 1.61 (19.00-24.44)	2.12 ± 0.06 (2.00-2.20)	2.51 ± 0.11 (2.30-2.70)
S. meridanus	No comparable call					
Slow, repetitious call						
S. g. griseicollis	No comparable call					
S. g. aburriacantor	No comparable call					
S. meridanus **Slow, repetitious call**	7/5: La Azulita (2/2) Paramo de Zumbador (1/1) and Guaramacal NP (1/1)	23.30 ± 20.25 (5.20-61.20)	180.86 ± 147.54 (42.00-441.00)	7.98 ± 1.74 (6.19-11.50)	3.41 ± 0.46 (2.70-4.20)	4.64 ± 0.26 (4.20-4.90)

Appendix 4: Vocal parameters of calls of "*S. griseicollis*" and "*S. infasciatus*"

Call type / *Taxon*	**No. of calls / no. of recordings: overall and by locality.**	**Length of call (s)**	**No. of notes in call**	**Notes/s**	**Max. frequency of first overtone in lowest note (kHz)**	**Max. frequency of first overtone in highest note (kHz)**
Trill						
"S. griseicollis"	61/10: Tamá (9/1), Rogitama (38/5), Suratá (3/1), Bojacá (8/1), Fusagasugá (2/1) and Montserrate (1/1).	1.01 ± 0.25 (0.35-1.45)	27.94 ± 8.42 (8.00-39.00)	26.54 ± 2.08 (20.00-29.50)	2.96 ± 0.31 (2.20-3.70)	3.74 ± 0.28 (3.00-4.20)
"S. infasciatus"	103/14: Chingaza (92/11); Soatá (4/2), Garagoa (7/1), .	1.23 ± 0.23 (0.55-2.00)	33.99 ± 7.87 (16.00-52.00)	28.28 ± 1.69 (25.22-31.81)	2.88 ± 0.24 (2.40-3.30)	3.16 ± 0.25 (3.20-4.10)
Reeling call						
"S. griseicollis"	22/6: Suratá (3/1), Iguaque (4/1), Fusagasugá (6/1) Monserrate (2/1), La Vieja (4/1) and Rogitama (3/1).	2.84 ± 4.05 (0.15-12.75)	70.33 ± 92.42 (4.00-294.00)	25.51 ± 3.39 (21.00-32.00)	2.55 ± 0.26 (2.20-2.90)	2.92 ± 0.20 (2.50-3.20)
"S. infasciatus"	26/10: Chingaza (23/9), Soatá (3/1).	3.52 ± 4.34 (0.40-13.35)	84.25 ± 98.20 (10.00-287.00)	26.24 ± 3.12 (21.50-30.91)	2.74 ± 0.13 (2.50-3.00)	2.41 ± 0.14 (2.20-2.70)
Churr						

"S. griseicollis"	32/4: Bogotá (1/1), Suratá (26/2), Iguaque (5/1).	1.58 ± 0.28 (1.05-2.00)	39.06 ± 5.89 (27.00-47.00)	24.80 ± 1.08 (23.10-26.67)	1.90 ± 0.11 (1.80-2.10)	2.81 ± 0.13 (2.50-2.90)
"S. infasciatus"	60/5: Chingaza (42/3), Soatá (18/2).	1.10 ± 0.27 (0.70-1.55)	24.54 ± 5.54 (15.00-33.00)	22.00 ± 1.26 (20.00-24.70)	2.24 ± 0.14 (1.90-2.50)	2.81 ± 0.19 (2.70-3.40)