NOTES ON TAPACULOS (PASSERIFORMES: RHINOCRYPTIDAE) OF THE EASTERN ANDES OF COLOMBIA AND THE VENEZUELAN ANDES, WITH A NEW SUBSPECIES OF *SCYTALOPUS GRISEICOLLIS* FROM COLOMBIA

Notas sobre tapaculos (Passeriformes: Rhinocryptidae) de la Cordillera Oriental de Colombia y los Andes venezolanos, con una nueva subespecie de *Scytalopus griseicollis* de Colombia

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ABSTRACT

We analysed biometrics, plumage and voice and inspected specimens to study the taxonomy of various high elevation tapaculos *Scytalopus* of the Eastern Andes of Colombia and the Mérida Andes of Venezuela. In light of a lack of any diagnostic vocal, plumage or biometric character, we propose treating *S. infasciatus* as a subjective junior synonym of *S. griseicollis*. *S. fuscicauda* and *S. meridanus* are indistinguishable by morphology, but we propose treating *S. fuscicauda* as a subspecies of *S. meridanus* in light of small observed differences in introductions to songs, which require further investigation. As the names were published contemporaneously, we propose priority for *S. meridanus* over *S. fuscicauda*. *S. meridanus* and *S. griseicollis* as redefined are each diagnosable vocally, supporting species rank for both of them. *S. griseicollis gilesi* subsp. nov. is described from the Yariguíes mountains. The new subspecies differs from *S. griseicollis* in its darker plumage, lower acoustic frequency scolds and longer tail. The recently discovered Eastern Andes population of *S. spillmanni* differs from Ecuadorian populations in its shorter tarsus length and slower song, meeting the requirements for some, but not all, subspecies concepts. With the status of *S. griseicollis, S. meridanus* and *S. spillmanni* populations clarified, it becomes apparent that two undescribed *Scytalopus* populations of the lower montane zone of the west slope of the Eastern Andes and Venezuelan Andes each await formal description. Other undescribed taxa apparently related to *S. griseicollis* or *S. meridanus* are present in Serranía del Perijá and the northern East Andes. Notes on geographical variation in *S. latrans* and *Myornis senilis* in the Eastern Andes are presented. Various proposed species and subspecies concepts for allopatric populations are discussed.

Key words: *Scytalopus*, tapaculo, new subspecies, species and subspecies limits, Colombia, taxonomy.

RESUMEN

Analizamos morfometría, plumaje, voces y especímenes para estudiar la taxonomía de varios tapaculos de altas elevaciones del género *Scytalopus* de la Cordillera Oriental de Colombia y la Cordillera de Mérida de Venezuela. Dada la ausencia de algún carácter diagnóstico en voz, plumaje o morfometría, proponemos tratar a *S. infasciatus* como un sinónimo subjetivo más joven de *S. griseicollis* . *S. fuscicauda* y *S. meridanus* son indistinguibles en su morfología, pero

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proponemos tratar a *S. fuscicauda* como una subespecie de *S. meridanus* debido a posibles pequeñas diferencias en la introducción de sus cantos, las cuales requieren mayor investigación. Como sus nombres fueron publicados contemporáneamente, proponemos la prioridad de *S. meridanus* sobre *S. fusciacuda*. *S. meridanus* y *S. griseicollis* (cada uno, como redefinidos) son vocalmente distinguibles, soportando su tratamiento como especies distintas. Describimos *S. griseicollis gilesi* subsp. nov. de la Serranía de los Yariguíes. La nueva subespecie difiere de *S. g. griseicollis* en su plumaje más oscuro, la frecuencia acústica más baja de los llamados y cola más larga. La recientemente descubierta población de *S. spillmanni* en la Cordillera Oriental difiere de las poblaciones ecuatorianas en su tarso más corto y canto más lento, cumpliendo los requerimientos de algunos, pero no todos, los conceptos de subespecie. Con la situación de las poblaciones de *S. griseicollis, S. meridanus* y *S. spillmanni* clarificada, es evidente que dos poblaciones de *Scytalopus* de la zona montana baja de la ladera occidental de la Cordillera Oriental y los Andes de Venezuela esperan ser descritas formalmente. Otro taxón sin describir, aparentemente relacionado con *S. griseicollis* o *S. meridanus*, se encuentra en la Serranía de Perijá. Se presentan notas sobre la variación geográfica en *S. latrans* y *Myornis senilis* en la Cordillera Oriental. Se discuten conceptos de especie y subespecie propuestos para poblaciones alopátricas.

Palabras clave: *Scytalopus*, tapaculo, nueva subespecie, límites de especie y subespecie, Colombia, taxonomía.

INTRODUCTION

Despite some recent research and new taxon descriptions, the tapaculos in the genus *Scytalopus* Gould, 1836 of the northern Andes remain among the most poorly understood bird taxa. Reasons for 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 and 2003; Cuervo et al. 2005). In a landmark study, Krabbe & Schulenberg (1997) demonstrated that various morphologically similar but vocally different populations replace one another by elevation or in different habitats and are best considered separate species Three new *Scytalopus* species have been described from Colombia in the last decade: Chocó Tapaculo *S. chocoensis*, Upper Magdalena Tapaculo *S. rodriguezi* and Stiles' Tapaculo *S. 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, 2007; 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) have increased the number of recognized species in the genus from around 10 to over 40 since the 1990s.

Birds reach among their greatest levels of diversity, intraspecific variation and terrestrial 'endemism' in the northern Andes (Stattersfield et al. 1998; Orme et al. 2005; Phillimore et al. 2007), but recent advances in *Scytalopus* taxonomy have largely resulted from research in Ecuador, which is only a small part of this region (Krabbe & Schulenberg 1997). Due to lack of recent field studies, our understanding of the genus *Scytalopus* in the Eastern Andes of Colombia remains based largely on early 20th century studies of museum specimens without associated vocal data (Chapman 1915, Hellmayr 1922, Zimmer 1939). In this paper, we assess the status of the taxa *S. griseicollis*, *S. infasciatus*, *S. meridanus* and *S. fuscicauda*, and discuss geographical variation in *S. spillmanni*, with particular reference to the Eastern Andes. We also describe a new subspecies of *S. griseicollis* from Serranía de los Yariguíes in Colombia and lay the foundations for several further new taxon descriptions.

STUDY AREA

The Eastern Andes (Cordillera Oriental) 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 centers of terrestrial avian endemism, with at least 35 bird species restricted to the range (Stattersfield et al. 1998). Our field surveys were concentrated in Serranía de los Yariguíes, with additional fieldwork in Santander, Boyacá and Cundinamarca departments of Colombia. Serranía de los Yariguíes forms a spur of the Cordillera Oriental, extending 100 km northwestward, rising to around 3400 m. The range is 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 2500m elevation. The high elevations of the Yariguíes had not been subject to ornithological study until our surveys (discussed in Donegan & Huertas 2005, Donegan et al. 2005 and 2007 and Huertas & Donegan 2006). The region was subsequently declared a National Park (see "Conservation" section below).

The following *Scytalopus* taxa were encountered during the Yariguíes study: White-crowned Tapaculo *S. atratus* (western slope 1300-1600 m); a presumably undescribed taxon related to *S. rodriguezi* (western slope 1700-2100 m; eastern slope 2000 m); Blackish Tapaculo *S. latrans* subsp. (western slope 1900-2900 m and eastern slope 2600 -2750 m); Pale-bellied Tapaculo *S. griseicollis* (western slope 2500-3000 m and eastern slope 3100 -3200 m); and a population related to Spillmann's Tapaculo *S. spillmanni* (western slope 2450-2900 m and eastern slope 2700 m). Data relating to specimens and sound recordings are set out in Appendix 1.

METHODS

MUSEUM STUDIES: In addition to studying the material we obtained in the field at Serranía de Yariguíes, we 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 Ornitológica 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 specimens held at American Museum of Natural History (AMNH); Museum of Comparative Zoology, Harvard University (MCZ); Field Museum of Natural History, Chicago (FMNH); Academy of Natural Sciences, Philadelphia (ANSP) and Carnegie Museum (CM), USA; and Museum für Naturkunde, Berlin, Germany (MFNU). The specimens (see Appendix 1) included 194 skins labelled as either "*S. griseicollis*", "*S. infasciatus*", "*S. meridanus*" or "*S. fuscicauda*" from the Colombian and Venezuelan Andes (excluding specimens bearing such labels but clearly of other species), as well as photographs of the type specimens of all of them. Plumage differences were noted by comparing specimens directly or by comparing photographs of specimens, in some cases taken with the same light box and camera alongside a standard white to black color array and correcting for darkness in Adobe Photoshop. In order to evaluate the degrees of isolation vs. overlap between certain taxa, specimen and sound recording localities were plotted, and models of potential distribution built using MAXENT 3.0 (Phillips et al. 2006) based on climate data obtained from Worldclim (Hijmans et al. 2005).

BIOMETRICS: We took the following measurements of each specimen: chord of closed wing, tail length (to nearest 0.5 mm), tarsus length, culmen from skull to tip of upper mandible (to nearest 0.1 mm) and, from specimen labels, mass (g) (Appendix 2). Data from birds in juvenile or immature plumage, undergoing moult from juvenile to adult plumage, or undergoing primary moult were excluded. Juveniles of these species were easily identified by their strongly and densely barred dark brown / whitish plumage throughout or in part, compared to a lack of barring (other than rufous / dark brown in the undertail region) in adults. Data for males only were subjected to principal components analysis (PCA) and analysis of diagnosability "levels" discussed further below, to exclude sex biases.

VOCAL ANALYSIS: Sound spectrograms, generated using the default settings of Raven Lite 1.0 (sometimes adjusted for brightness, expanded to show up to c. 5kHz and 2-5 seconds), were studied from unpublished and published sound recordings from plausible localities of *S. spillmanni*, *S. griseicollis*, *S. infasciatus*, *S. meridanus* and *S. fuscicauda* in order to assess the taxonomic status of new populations of *S. spillmanni* and *S. griseicollis* discovered during our Yariguíes fieldwork, given that any description could potentially otherwise be criticized as a result of the uncertain status of *S. meridanus, S. fuscicauda* and *S. infasciatus*. Songs and calls subject to study were defined as sequences of notes broken by gaps significantly longer than the intervals between individual notes of a sequence. Multiple calls were measured from single recordings and localities when available in order to determine the full range of variables. Recordings of scolds of individuals recorded in natural conditions and following playback were included for the same reason. Only scolds, rattles and alarm calls (not songs) were given directly in response to playback by the taxa subject to vocal analysis in the Yariguíes; thus, song data are likely not to include a significant number of unnaturally stimulated individuals. Data on numbers of recordings and spectrograms, together with a gazetteer of recording localities, are presented for each taxon and call studied in Appendix 3.

The taxa studied make various calls, all of which

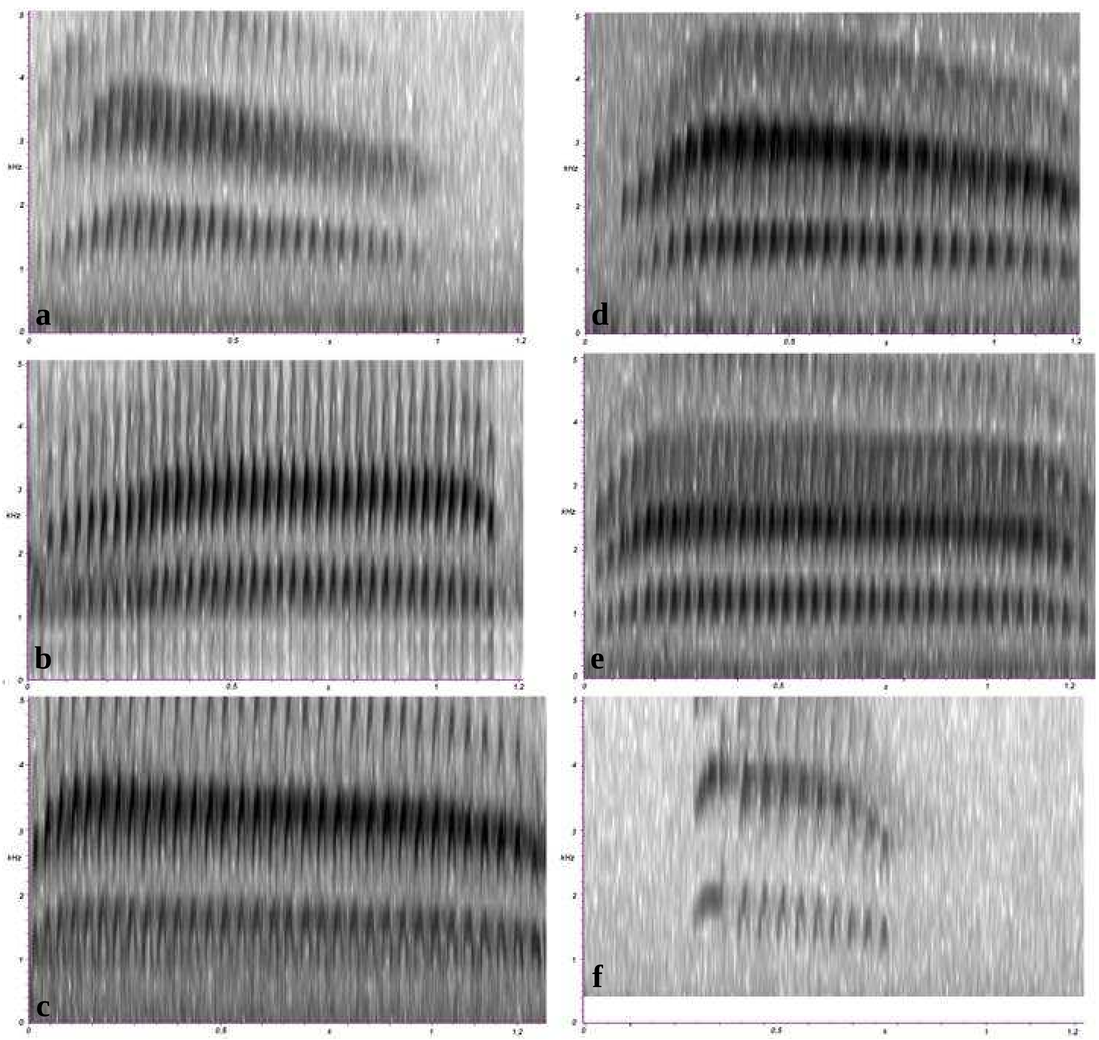

Figure 1: Spectrograms of scolds of *S. griseicollis* and *S. g. gilesi*. a) *S. griseicollis* undescribed *subsp.* PNN Tamá, Apure, Venezuela (C. Parrish recording no. 6079 on www.xeno-canto.org); b) *S. g. griseicollis* (="*S. infasciatus"*) PNN Chingaza, Cundinamarca, Colombia (J. Parra-B. recording); c) *S. g. griseicollis* Rogitama, Boyacá, Colombia (J. Zuluaga recording). d) *S. griseicollis gilesi*, Filo Pampona, Serranía de los Yariguíes (TMD recording); e) *S. griseicollis gilesi*, Alto Cantagallos (TMD recording). f) curtailed scold of *S. griseicollis* undescribed *subsp.*, La Pajita, Bucaré Suratá, Santander 3,300 m (JEAC recording, 15 March 2006. Variation in song shape is individual.

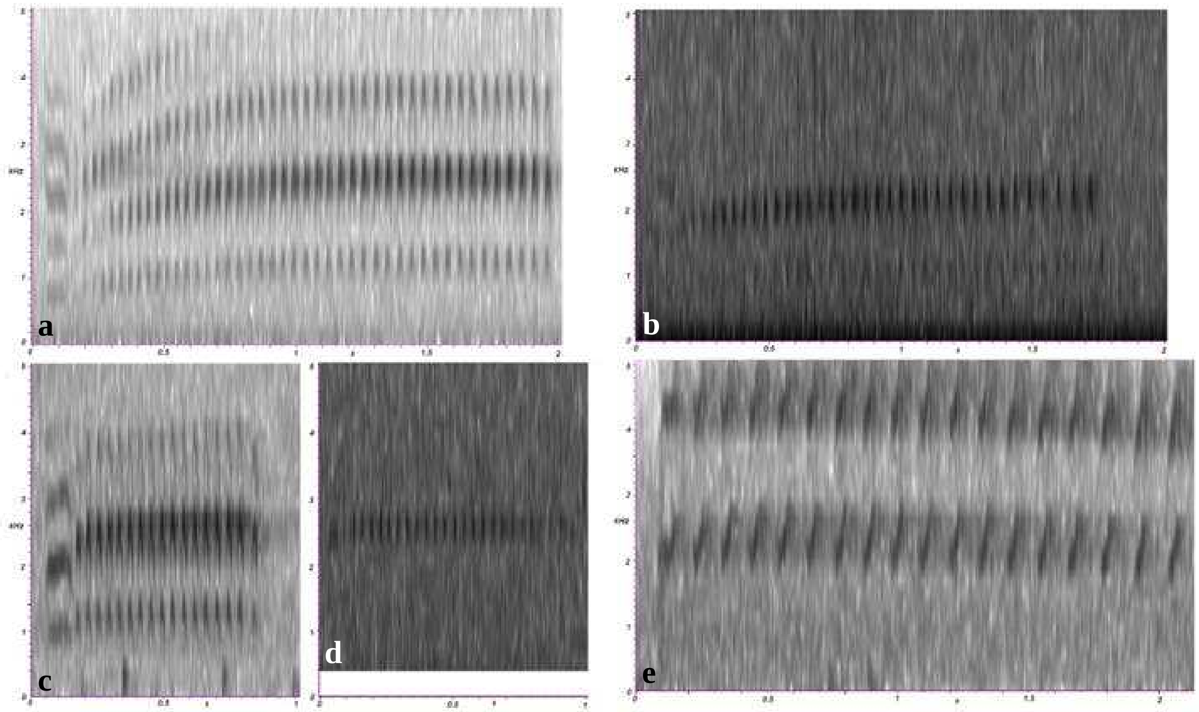

Figure 2: Spectrograms of reeling songs of *S. griseicollis* and related taxa (or extracts thereof): a) rising reeling song of *S. griseicollis* undescribed *subsp.* (JEAC recording Suratá, Santander, 15 March 2006, at 3300 m elevation at La Pajita Farm, Vereda Bucaré, Santander) with accentuated first overtone and flat "zz" at start of call; b) rising reeling song of *S. griseicollis gilesi* (TMD recording at Filo Pamplona type locality, Yariguíes, July 2005) which lacks the accentuation of the second overtone but includes the initial "zz", barely visible on spectrogram at start of call; c) flat reeling song of *S. griseicollis* ("*S. infasciatus*") from PNN Chingaza, Cundinamarca, Colombia (J. Parra recording), also with introductory "zz"; d) flat reeling song of *S. griseicollis gilesi* with initial "zz" (TMD recording, Lepipuerto, Yariguíes, January 2005); e) reeling song of *S. meridanus* for comparison (Boesman 1999: Páramo de Batallón, Táchira state, Venezuela, 2700-2900 m).

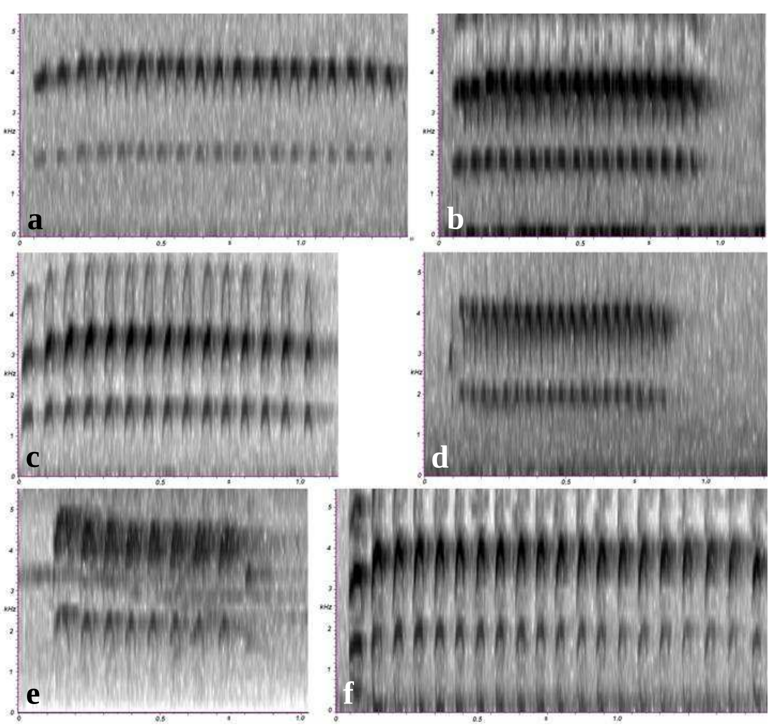

Figure 3: Scolds of *S. spillmanni* taxa and "*S. cf. canus opacus sp.*". a) *S. spillmanni* Eastern Andes (a slower example: J.E.A.C. recording, La Aurora type locality, Yariguíes, Santander, Colombia; b) *S. spillmanni* Eastern Andes (a faster example: TMD recording, Lepipuerto, Yariguíes, Santander, Colombia); c) *S. spillmanni* Central Andes (O. Laverde recording: Reserva Natural Ibanasca, Ibagué, Tolima, Colombia, IAVH 24245); d) *S. cf. canus opacus sp.* (N. Krabbe recording, east slope of Cerro Toledo, Zamora-Chinchipe, Ecuador: track 10.38 in Krabbe & Nilsson 2004); e) *S. spillmanni* Ecuador (N. Krabbe recording; Quebrada Las Ollas, Sucumbíos, Ecuador: track 44.3 in Krabbe et al. 2001); f) *S. spillmanni* Ecuador (N. Krabbe recording, San José, Tandayapa ridge, Pichincha, 2300m: track 9.16 in Krabbe & Nilsson 2004).

consist of rapidly repeated up-down, up, or down strokes. The most common calls comprise: (i) short scolds which rise and then fall in acoustic frequency ("scold") (e.g. Figs. 1 & 3); (ii) rising or flat reeling songs which either rise or are relatively constant in acoustic frequency and which may be very short or long (up to over a minute) in duration ("reeling song") (e.g. Figs. 2, 4 & 5). *Scytalopus spillmanni* taxa also make explosive, short "brzk" calls and females give what Krabbe & Schulenberg (1997) term an "advertising call". *Scytalopus meridanus* has been reported making short call notes (Krabbe & Schulenberg 1997, Boesman 1999). *Scytalopus griseicollis* rarely makes a slower, higher frequency version of its scold (Fig. 1). *S. griseicollis* and *S. spillmanni* also give unmusical rattles, similar to the scold but with less clearly-defined and higher frequency individual notes. Only songs and scolds were subject to detailed analysis, on account of small sample sizes for other vocalizations. Scolds are given in response to playback and apparently have a territorial function. Songs appear likely to be more relevant to mate selection but are given year-round and may also have a territorial function.

Various vocal variables described by Isler et al. (1998, 1999, 2006, 2007, 2008) were considered for further analysis in a preliminary study of spectrograms. Variables which showed variation between individuals, spectrograms, or populations were subject to further analysis, whilst apparently

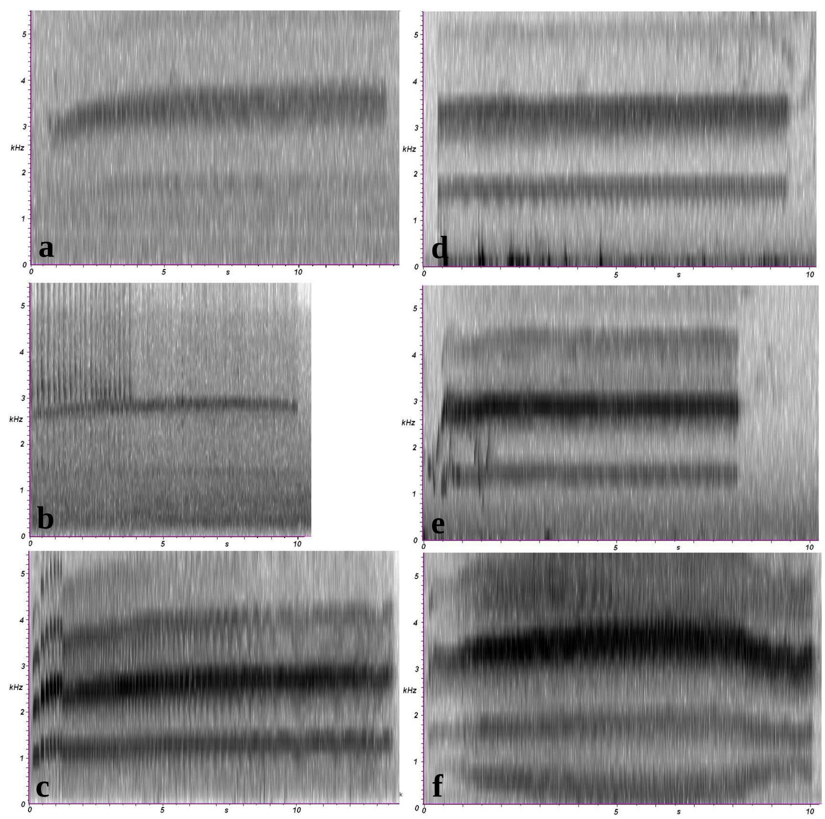

Figure 4: Reeling songs of *S. spillmanni*. Left: elongated rising reeling songs of a) *S. spillmanni* Eastern Andes (J.E.A.C. recording, La Aurora, Yariguíes, Santander, Colombia); b) *S. spillmanni* Central Andes (L. E. Urueña recording, Ibagué, El Rancho, road to Nevado del Tolima, Tolima, Colombia); and c) *S. spillmanni* in Ecuador (N. Krabbe recording, Las Palmas, Cotopaxi; recording 44.1 in Krabbe et al. 2001). Right: elongated "flat" reeling songs of d) *S. spillmanni* Eastern Andes (O. Laverde recording: Fusagasugá, Cundinamarca, Colombia, IAVH 17856); e) *S. spillmanni* Central Andes (O. Laverde: Reserva Natural Ibanasca, Ibagué, Tolima, Colombia, IAVH 24179); and f) *S. spillmanni* Ecuador (N. Krabbe recording: San Jose, Tandayapa ridge, Pichincha, 2300m). Variation in acoustic frequency over time between different spectrograms and other differences are subject to individual, not geographic, variation. However, note the lower frequency Central Andes recordings compared to the Eastern Andes (compared top two and middle two recordings); and the elaborate introduction to the rising reeling song in Ecuador (bottom left) not found to such an extent in an any of our Eastern or Central Andes recordings (although this introduction is often absent in Ecuadorian recordings also).

constant variables and those inappropriate for study were discarded. For example, due to calls and songs being composed of a number of individual notes of the same volume but different acoustic frequencies, frequency variables defined with reference to a "principal" note were not amenable to study. Measurements of frequency bandwidths were avoided because individual notes in the calls of several taxa have short, quiet "tails" to the upstroke, downstroke, or both, meaning that the lowest recorded point on a spectrogram is biased by the quality of recording equipment and distance of a bird from the observer. The maximum point provides a more consistent reference point for these birds. The following variables were selected for further study as apparently varying between different populations or individual calls: total number of notes in call (n); total song duration (s); song speed or pace (average number of notes per second: by dividing number of notes in song by song duration); maximum acoustic frequency of lowest note; maximum frequency of highest note; variation in frequency (the difference between the latter two measurements, all in kHz); and subjective description of note shape. Of the various selected variables, number of notes, song duration and frequency variation showed far greater intra- than interspecific variation and a maximum frequency of lowest note was correlated within populations with the maximum frequency of highest note. None of these variables were subject to further analysis.

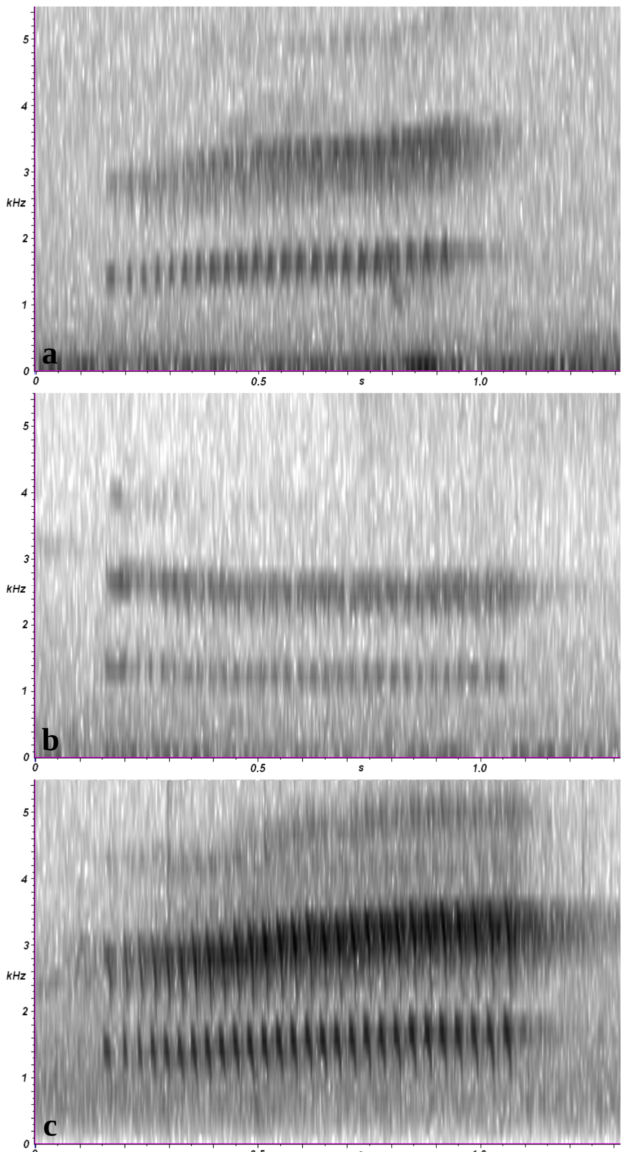

Figure 5: Examples of curtailed reeling songs of *S. spillmanni*. a) *S. spillmanni* Eastern Andes (J.E.A.C. recording, La Aurora, Serranía de los Yariguíes, Santander, Colombia); b) *S. spillmanni* Central Andes (O Laverde recording, Río Blanco, Caldas, Colombia); c) *S. spillmanni* Ecuador (N. Krabbe recording, Ecuador, Krabbe et al. 2001). Note the downstrokes in the Ecuadorian recording, not found in East Andes recordings, but Ecuador recordings include songs of similar note shape to East and Central Andes birds.

In order to assess the validity of the putative taxon "*S. infasciatus*" and differences between other populations, *S. griseicollis / infasciatus* recordings were split into four subsets: (i) eastern Cundinamarca and Boyacá (Iguaque region); (ii) Bogotá region, western Cundinamarca and Boyacá; (iii) Serranía de los Yariguíes; and (iv) northern sites (Santander, Norte de Santander, and Venezuela). Data for *S. fuscicauda* (Lara state) and *S. meridanus* (other states in Venezuela) were also considered separately. For *S. spillmanni* populations, data were split into the following geographical subsets, after excluding data from inter-Andean sites in Ecuador: (i) Colombian Central Andes; (ii) Colombian Eastern Andes; (iii) western slope of Ecuador; (iv) eastern slope of Ecuador. Western Andes recordings and biometrics for *S. spillmanni* were not considered in detail as such populations are the subject of separate studies (Cuervo et al. 2004; Krabbe et al. 2006). Some of the above subsets of data were subject to further splitting and analysis to assess possible clinal and elevational variation.

STATISTICAL TESTS: For means and standard deviations (Appendix 3) and diagnosability analyses

(Appendix 4) we used a reduced data set with only the first three spectrograms for which full data were available from each recording. Various diagnosability tests were assessed for pairs of vocal variables of different populations for song speed and maximum acoustic frequency of songs and scolds and biometric data.

LEVEL 1: Statistically significant differences at $p<0.05$. A Bonferroni correction was applied fo both vocal data (6 variables) and biometrics (5 variables), to produce testwise significance levels of $p<0.0083$ and $p<0.01$ respectively. For acoustic frequency data, an unequal variance (Welch's) *t*-test was used; for speed data, both Kolmogorov-Smirnov and Mann-Whitney U tests were used. These calculations consider statistical significance of differences, but tolerate a considerable degree of overlap.

Various further calculations described below were also carried out to measure differences between populations in the context of various proposed or possible species and subspecies concepts. In the formulae used below, $\bar{x}_1$ and s_1 are the sample mean and sample standard deviation of Population 1; $\bar{x}_2$ and s_2 are the sample mean and sample standard deviation of Population 2; and t is the value of t using one-sided confidence intervals at the percentage specified for the lower of the degrees of freedom of the two populations for the relevant variable, with t_1 referring to Population 1 and t_2 referring to Population 2.

LEVEL 2: Hubbs & Perlmutter (1942)'s now little-used subspecies concept, as modified. Sample mean of Population 1 falls outside range of 95% of Population 2 (or sample means two standard deviations apart, controlling for sample size):

$$|(\bar{x}_1 - \bar{x}_2)| > (s_1(t_{1\ @\ 97.5\%}) + s_2(t_{2\ @\ 97.5\%}))/2$$

LEVEL 3: The traditional 75%/99% test for subspecies diagnosability (Amadon 1949; Patten & Unitt 2002), modified to control for sample size:

$$|(\bar{x}_1 - \bar{x}_2)| > s_1(t_{1\ @\ 99\%}) + s_2(t_{2\ @\ 75\%})$$

and

$$|(\bar{x}_2 - \bar{x}_1)| > s_2(t_{2\ @\ 99\%}) + s_1(t_{1\ @\ 75\%})$$

LEVEL 4: Diagnosability based on recorded values (first part of Isler et al. 1998's diagnosability test).

LEVEL 5: 95% / 95% diagnosability or sample means four standard deviations apart controlling for sample size (second part Isler et al. 1998's diagnosability test):

$$|(\bar{x}_1 - \bar{x}_2)| > s_1(t_{1\ @\ 97.5\%}) + s_2(t_{2\ @\ 97.5\%})$$

CRITERIA APPLIED FOR ASSESSING SPECIES AND SUBSPECIES RANK: Helbig et al. (2002) advocated the general principle, previously discussed by some other authors cited therein, that in order to assess the rank of allopatric populations, a comparison with closely-related sympatric or parapatric populations known to be good species should be undertaken. Isler et al. (1998, 1999, 2006, 2007, 2008), in studies of species limits using voice for suboscine passerines, suggested assigning species rank to allopatric antbird populations where three or more measured vocal variables for loudsongs differed diagnosably, based on observed differences between closely related sympatric species in that family. A useful comparison for assessing *Scytalopus* species limits is provided between the *S. spillmanni* population recently discovered in the Eastern Andes (Donegan et al. 2007) and *S. griseicollis*, which have similar calls and replace one another in elevational or habitat parapatry and for which we have a large sample of recordings. Isler et al.'s diagnosability test (Levels 4 and 5) was met for *S. griseicollis* and the Eastern Andes population of *S. spillmanni*, but for one vocal variable; and only for scolds, not songs (cf. Bornschein et al. 2007). For songs, some shape features are likely to assist identification: for example, introductory notes to songs (if present), but these are not found on all recordings. *Scytalopus griseicollis* and Eastern Andes *S. spillmanni* also differ in plumage. We propose supplementing Isler et al.'s diagnosability test with consideration of the statistical significance of differences (Level 1). We therefore ranked allopatric populations as species where they show Levels 1, 4 and 5 diagnosability for songs or scolds based on at least one vocal variable and treat populations as conspecific if they do not meet this test.

Possible criteria for defining subspecies limits in *Scytalopus* have been little explored. Vocalizations in suboscines such as *Scytalopus* are considered to be innate and stereotypical (Kroodsma 1984; Whitney 1994; Cuervo et al. 2005). Differences in voice between populations may therefore have a genetic basis. Isler et al. (*op. cit*.) applied a "diagnosability of one character" test (whether vocal, biometrics or plumage) for subspecies in Thamnophilidae (Level 4/5: essentially a phylogenetic species with small differences not meriting species rank). The traditional test in ornithology for diagnosing subspecies is our Level 3 "99+%/75%" test. Luckow (1995) has alternatively proposed ranking allopatric populations with statistically significant means (our Level 1 diagnosability) as subspecies. This approach has been applied to some recent bird subspecies descriptions where statistically significant differences are shown for a range of biometric and plumage variables (e.g. Stiles & Caycedo 2002).

We do not propose new criteria to delimit species or subspecies for allopatric taxa. We therefore conservatively propose the recognition of new subspecies only if allopatric taxa meet Levels 1, 2, 3 and 4/5 diagnosability for at least one character (i.e. satisfy all mentioned subspecies definitions). We propose synonymy at subspecies level only if two allopatric populations fail to achieve any level of diagnosability. Other putative subspecies are discussed but are not described, pending further discussion of the use of subspecies concepts in ornithology. We also consider in this paper the status of an isolated population that is phenotypically differentiated but not genetically diagnostic from allopatric populations. Proponents of a biological species concept (Helbig et al. 2002; Remsen 2005) recommend ranking such taxa as subspecies. Proponents of phylogenetic species concepts have proposed ranking such taxa as species (Zink 2005).

SCYTALOPUS TAPACULOS IN THE EASTERN ANDES OF COLOMBIA

The status of *Scytalopus infasciatus* and *S. griseicollis*

The Pale-bellied (or Matorral or Rufous-rumped) Tapaculo *S. griseicollis* (Lafresnaye, 1840) and Colombian (or Cundinamarca) Tapaculo *S. infasciatus* Chapman, 1915 are both recorded from the Eastern Andes of Colombia. Both have rather light gray plumage compared to congeners and occur generally at high elevations. Zimmer (1939) treated *S. infasciatus* as a synonym of *S. griseicollis* and was followed by Peters (1951). However, *S. infasciatus* has been ranked as a species by some authors (e.g. Chapman 1915; Krabbe & Schulenberg 1997; Asociación Bogotana de Ornitología 2000; Gill & Wright 2006), but Krabbe & Schulenberg (1997) noted that comparison of material from the Eastern Andes with the type of *infasciatus* would be necessary before its status could be fully resolved. These same authors later (2003) treated *S. infasciatus* as a subspecies of *S. griseicollis*, but restricted the former to a single site and noted that the two taxa might be synonymous. Remsen et al. (2008) and Salaman et al. (2007) followed this treatment.

The type specimens 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. The juvenile has strong barring throughout. The other specimen has acquired almost complete adult plumage but retains strong barring on the flight feathers. Although it is never possible to be certain with "Bogotá" skins, these specimens may have 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 Páramo de Beltrán, on the eastern slope of the Eastern Andes in Cundinamarca department, some 15 km east of Bogotá and now in Parque Nacional Natural (PNN) Chingaza. The only unique distinguishing feature of *S. infasciatus* per the original description is its darker underparts compared to *S. griseicollis*. Other features of the holotype, such as barring on the vent, were considered probably due to age-related variation as such features were also observed in *S. griseicollis* (Chapman 1915). It has been hypothesized 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* is more common in drier or secondary habitats, with *S. infasciatus* present in more humid habitats or better-conserved forest (Asociación Bogotana de Ornitología 2000). The darkness hypothesis is considered further below. The "barring" hypothesis has some support from the type specimen but was rejected by Chapman (1915) in the type description and appears to involve merely age-related variation. Having observed and sound recorded individuals of identical song on different mountain slopes and in drier, more humid, primary and disturbed habitats of the Eastern Cordillera, we can also reject the “habitat” hypothesis.

Although we were unable to make direct comparisons, the *S. infasciatus* holotype appears unexceptional in its plumage. Its dorsal and ventral plumage are within the range of variation of specimens at ICN and other museums assigned to either *S. griseicollis* or *S. infasciatus*. A recent plate of "*S. infasciatus*" (Krabbe & Schulenberg 2003) exaggerates considerably the darkness of the plumage of the type. Twelve recently-collected and older Eastern Andes *Scytalopus* specimens, including from PNN Chingaza / Páramo de Beltrán region do not differ significantly in their plumage from Bogotá region specimens in the ICN. Darker skins previously labelled *S. infasciatus* and lighter ones previously labelled *S. griseicollis* at ICN come from a variety of localities and regions. Dark / light plumage is not strongly linked to sex differences, with intra-sex variation exceeding inter-sex variation. There is no clear division of the series inspected into “darker” and “lighter” specimens, nor into barred or unbarred specimens; rather, there is a continuum of plumage variation. A similar extent of variation in underpart coloration and barring is evident in the series of *S. meridanus* inspected and within our three specimens of the Yariguíes population of *S. griseicollis*. No statistically significant (Level 1) differences in biometrics were noted between specimens from Iguaque and the Bogotá region.

Flat and rising reeling songs and scolds are given by *S. griseicollis / infasciatus* populations throughout the Eastern Andes with no geographical separation of such song types. A sample including 12 recordings of reeling songs and 11 of scolds (with many more spectrograms) from PNN Chingaza region are not diagnosable (even to Level 1) from western Cundinamarca or Boyacá recordings. Also, no known geographic barrier exists between páramos in PNN Chingaza and those in hills above Bogotá that might act to isolate *S. griseicollis* from “*S. infasciatus*”. Given the lack of statistically significant differences in plumage, biometrics or voice between populations from the region of the *S. griseicollis* and *S. infasciatus* type localities, the similarity of type specimens and lack of any obvious isolating barrier, we concur with Krabbe & Schulenberg (2003) that *S. griseicollis* and *S. infasciatus* should be treated as conspecific. In addition, since it fails to meet the requirements for any of the subspecies concepts mentioned above, we consider *infasciatus* to be a subjective junior synonym of *S. griseicollis*.

A new subspecies of *Scytalopus griseicollis*

The isolated Serranía de los Yariguíes population of *S. griseicollis* shows diagnostic plumage and biometric differences and statistically significant mean vocal differences from populations in the main Eastern Andes. We therefore describe it as:

***Scytalopus griseicollis gilesi*, subsp. nov.**

HOLOTYPE.– Adult male (Fig. 6), collected by the authors and prepared by J. Avendaño-C. (field number JEAC 297) on 13 July 2005 in páramo at Filo Pamplona above La Aurora, vereda San Isidro, Municipality of Galán, Santander Department, Colombia (06º38’N; 73º24’W; 3200 m) on the eastern slope just below the main ridgeline of the Yariguíes massif. It is deposited at the Instituto de Ciencias Naturales, Universidad Nacional, Bogotá, Colombia (no. ICN 35609). Tissue samples (heart) and a

Figure 6: The holotype of *S. g. gilesi*. Photographs by B. Huertas/Proyecto YARE.

skeleton were deposited at the Museo de Historia Natural at Universidad de los Andes in Bogotá. Sound recordings of the holotype prior to capture are deposited at IAVH and the British Library and are available at www.xeno-canto.org (XC 18452, 18453, 18454, 18455 and 18456).

DIAGNOSIS.– *Scytalopus griseicollis gilesi* exhibits all the characteristics of the genus *Scytalopus* (Ridgway 1911; Krabbe & Schulenberg 1997; Cuervo et al. 2005). It appears to be most closely related to *S. griseicollis* and *S. meridanus* on account of its rather gray plumage and orange-rufous vent, similar calls and a páramo and subpáramo habitat of the Eastern Andes of Colombia. A preliminary molecular study found a specimen of each of *S. g. griseicollis* and *S. g. gilesi* to share the same mtDNA haplotype for the second subunit of the NADH deshydrogenase gene (ND2; C.D. Cadena in litt. 2007).

Scytalopus griseicollis gilesi is diagnosable from *S. griseicollis* populations by its darker and less brownish back and tail and its darker, more slate gray, underparts (Fig. 7). It also differs from the nominate in its longer tail (Levels 1, 2 and 4; or 4 only compared to the undescribed northern subspecies discussed below), slower and lower song (Level 1) and lower frequency scold (Level 1; Levels 1, 2 and 4 compared to the northern subspecies: Fig. 1). Yariguíes specimens cluster separately from those of other Eastern Andes populations in PCA (Fig. 9), but a larger sample might show some overlap. We did not hear long reeling songs (cf. up to 15 seconds given by nominate *S. griseicollis*) at any of our study sites (Level 1; also *F*-test, $p<0.01$).

The new subspecies does not appear to represent the extreme of a cline. We have inspected specimens and sound recordings of nominate *S. griseicollis* from the Eastern 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. Chavarro & J. Zuluaga sound recordings), each of which are *c*.60 km from Serranía de los Yariguíes in the main section of the Eastern Andes. These sound recordings and specimens are consistent with those of *S. g. griseicollis* and the unnamed northern subespecies respectively.

Scytalopus griseicollis gilesi can be distinguished from *S. meridanus* of the Venezuelan Andes by its lower song and faster and lower scold (up to Level 5, in each case), different note shape (Level 4), longer wing (Levels 1, 2, and 4), and longer tail (Levels 1 and 4) (Fig. 8). It differs from *S. spillmanni* populations to varying degrees in its lighter plumage, slower reeling song, faster trill, shorter wing, shorter tarsus, and lower mass (see Appendix 4 for details). *Scytalopus g. gilesi* shares a number of morphological and vocal features with the Central Andes population of *S. spillmanni*, the songs of which overlap for all measured variables. The only recent Central Andes specimen of *S. spillmanni* studied is lighter plumaged than southern and eastern populations of the same species, whilst *S. g. gilesi* is a darker version of *S. griseicollis*. However, the diagnostic difference in scold speed requires species rank between these populations.

DESCRIPTION OF THE HOLOTYPE.– Color nomenclature follows Munsell Color (1977; 2000). Bill black (not coded); ventral proximal lower mandible slightly lighter at base (Gley 1 7/N); iris dark brown (10R 3/3); head, mantle and tail dark gray-brown (7.5YR 2.5/2); underparts to breast gray (Gley 1 3/N), becoming slightly lighter (Gley 1 4/N) on lower belly; wing coverts and flight feathers dark gray (7.5YR 2.5/2) with tertials tipped ochraceous brown (5YR 3/4), with dark gray (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 gray (7.5YR 2.5/2); tarsus reddish dark gray (5YR 4/3) frontally, behind lighter (10R 3/1); Foot soles grayish 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: maximum flattened wing (field) 62, wing chord (skin) 58, tail 45, tarsus 22.5, total culmen 13.5, exposed culmen 11.0; mass 18.0g.

PARATYPES AND OTHER MATERIAL.– We designate the following paratypes: (1) Immature male no. ICN 35610, collected by the authors and prepared

Figure 7: Dorsal and ventral views of (left to right): (i) *S. g. gilesi* holotype; (ii) *S. g. gilesi* Pamplona paratype; (iii) Specimens of *S. g. griseicollis* ICN 34780 (male, Cundinamarca, Bogotá, Cerros Orientales, La Aurora, collected on 15/11/2003 by F.G. Stiles); (iv) ICN 34492 (female, Cundinamarca, Bosque de Toma, Cerros Orientales de Bogotá, 3050m, collected on 1 April 1993 by A. Guttiérez & S. Rojas, labelled "*griseicollis*" and an example of one of the lighter specimens); (v) ICN-31235 (male, Cundinamarca, Chingaza, Piedras Gordas; collected by F.G. Stiles on 1 November 1991, a relatively dark bird formerly labelled "*infasciatus*"); (vi) ICN 19623 (male, Cundinamarca, Bogotá, Monserrate, collected by P. Bernal on 19 June 1968). Photographs at ICN by TMD.

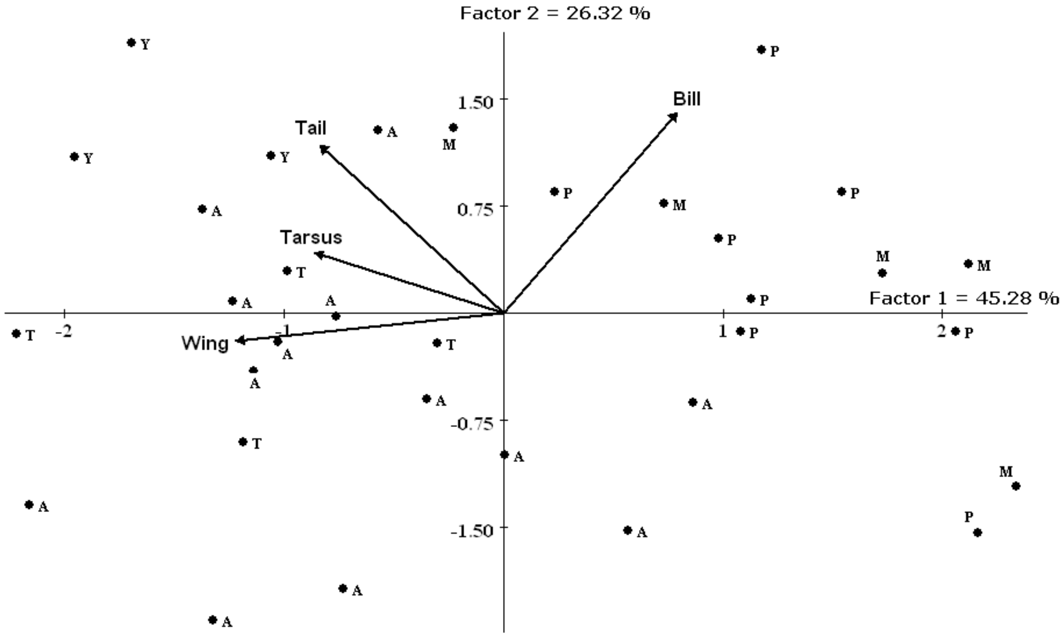

Figure 8: Principal Component Analysis using bill, tail, tarsus and wing data for adult males only of *S. griseicollis* ("A": all Eastern Andes north to Santander), *S. meridanus* ("M": all Venezuelan Andes), *S. sp.* of Perijá ("P": all Perijá range of Eastern Andes), *S. griseicollis* undescribed *subsp.* from the Santander-Tamá region ("T": Eastern Andes in Norte de Santander, Colombia and Apure, Venezuela) and *S. g. gilesi* ("Y").

by T. Donegan on 14 July 2005 at the Filo Pamplona type locality. Tissue samples (heart) and a skeleton have also been deposited at Universidad de los Andes. (2) Adult male no. ICN 36175, collected and prepared by J. Avendaño-C. (JEAC 377) on 12 November 2006 on a stunted ridge above 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 Universidad de los Andes (ver Fig. 7).

The Pamplona paratype had smaller testes (left: 3 x 1.5mm; right: 2.5 x 1.5mm) than the holotype. As the latter was collected just a few days earlier and was in breeding condition, it is possible that the paratype was a younger bird. It has darker gray underparts than the holotype (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: maximum flattened wing (field) 61, wing chord (skin) 56, tail 44, tarsus 22.0, total culmen 13.5, exposed culmen 11.0, mass 17.5 g. Stomach contents included Coleoptera exoskeleton remains. The Alto Cantagallos male had rather large testes (left: 4.6 x 2.7mm; right: 4.2 x 3.2mm). It is similar to the holotype in its coloration but lacks barring on flanks and undertail coverts. Barring on the vent is a character that is also variable in nominate *S. griseicollis* (Chapman 1915) and *S. meridanus* (see above). Measurements in mm are as follows: maximum flattened wing (field) 57, wing chord (skin) 57, tail 44, tarsus 23.0, full culmen 13.2, exposed culmen 9.3.

We, E. Briceño and B. Huertas have observed individuals consistent with the type series at very close quarters on approximately 20 occasions during three weeks' total fieldwork at sites at which the species was relatively common in the Yariguíes.

ETYMOLOGY.– This bird is named for O. A. Robert Giles of Wimbledon, London, UK. His name is formed as a fictional first declension masculine Latin noun and declined in the genitive singular. Robert is a keen birder and conservationist and a friend of the first author. He is among the founders and a member of the Consejo of Fundación ProAves, a bird conservation NGO based in Colombia, and is chairman of Ecoturs S.A., an ecotourism organization operating in Colombia that donates all its profits to ProAves. Robert has supported many conservation initiatives in Colombia. In particular, Robert's support was crucial in providing seed funding for various ProAves nature reserve purchases, including for the reserve in Serranía de los Yariguíes near where this new tapaculo is found.

ECOLOGY.– *S. g. gilesi* is a skulking bird observed most frequently foraging in dense shrubs of páramo and subpáramo ridgetop habitat up to 2 m above ground level. Stomach contents suggest it is insectivorous, typical of the genus. It seems to be most numerous in slightly taller scrub found in sheltered alcoves, along exposed ridges and just above the treeline. The area is subject to quite extraordinary levels of precipitation and near-constant ground-level cloud (fog). Our own rainfall readings taken in the field and data in Worldclim (Hijmans et al. 2005) reveal higher levels of precipitation for sites where *S. g. gilesi* is predicted to be present in Serranía de los Yariguíes than the average for sites where *S. g. griseicollis* is predicted to be present in the Eastern Andes (average 1400 vs. 1900 mm/year; Welch's t, $p<0.001$, d.f.=523). The humid habitats of *S. g. gilesi* may have given rise to a darker population, per "Gloger's rule" (Zink & Remsen 1986). Plants found in *S. g. gilesi*'s habitat include Blechnaceae (*Blechnum schomburgkii*), Eriocaulaceae (*Paepalanthus*), Ericaceae, Clusiaceae, Bromeliaceae, Melastomataceae, Orchidaceae, unusual Asteraceae (*Espeletia*) and some isolated tall palms (Arecaceae). At Alto Cantagallos (2450m) on the western slope, *S. g. gilesi* was present along an exposed ridgetop only, which presented stunted vegetation (2m high "canopy") including short, gnarled, winding trees and *Espeletia* of apparently the same species as in the páramo.

At Alto Cantagallos and Lepipuerto, *S. g. gilesi* was heard calling only in the ridgetop páramo and treeline habitat in small bushes and shrubs; in mossy montane cloud forest below the treeline, it was replaced sharply by *S. latrans* and *S. spillmanni*. Calling males of *S. g. gilesi* on the one hand and *S. latrans* and *S. spillmanni* on the other were sometimes audible within 10 m of one another at the treeline, but never were found together in the same habitat. *Scytalopus g. gilesi* was common in the páramo of Filo Pamplona, 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, characterized by tall emergent trees, an open canopy with little midstorey and thick bamboo (Poaceae: *Chusquea*) understory. Below this elevation, it was again replaced by *S. latrans* and *S. spillmanni*.

DISTRIBUTION.– We recorded *S. g. gilesi* at high elevations along almost the entire length of Serranía de los Yariguíes in three municipalities (Fig. 9). However, no skins of this taxon exist in collections from the main Eastern Andes: apparently it is endemic to the Yariguíes range. Although *S. griseicollis* was recently sound recorded as low as 1300 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. Above this elevation, the Yariguíes massif is separated from the main Andean cordillera to the south by some 50km of 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 valleys of the Magdalena, Sogamoso and Suárez rivers. *Scytalopus griseicollis* has been collected and sound recorded at sites close to this ecological divide in the main Eastern 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 brief observations in which no *Scytalopus* were recorded; Fundación Natura 2003). Figure 10 suggests elevational connectivity of that site with localities where *S. g. griseicollis* populations are found.

CONSERVATION.- Although bird conservation assessments often consider only species level taxa (e.g. BirdLife International 2004), distinctive subspecies such as *S. g. gilesi* are of conservation relevance (e.g. Peterson & Navarro-Sigüenza 1999; Zink 2003). An assessment of the new taxon's conservation status therefore follows. The area of occurrence of *S. g. gilesi* is rather difficult to determine because it occurs principally in the ecotone between páramo and forest, which does not correspond to any elevational band but rather varies in width and elevation with topography and on differ-

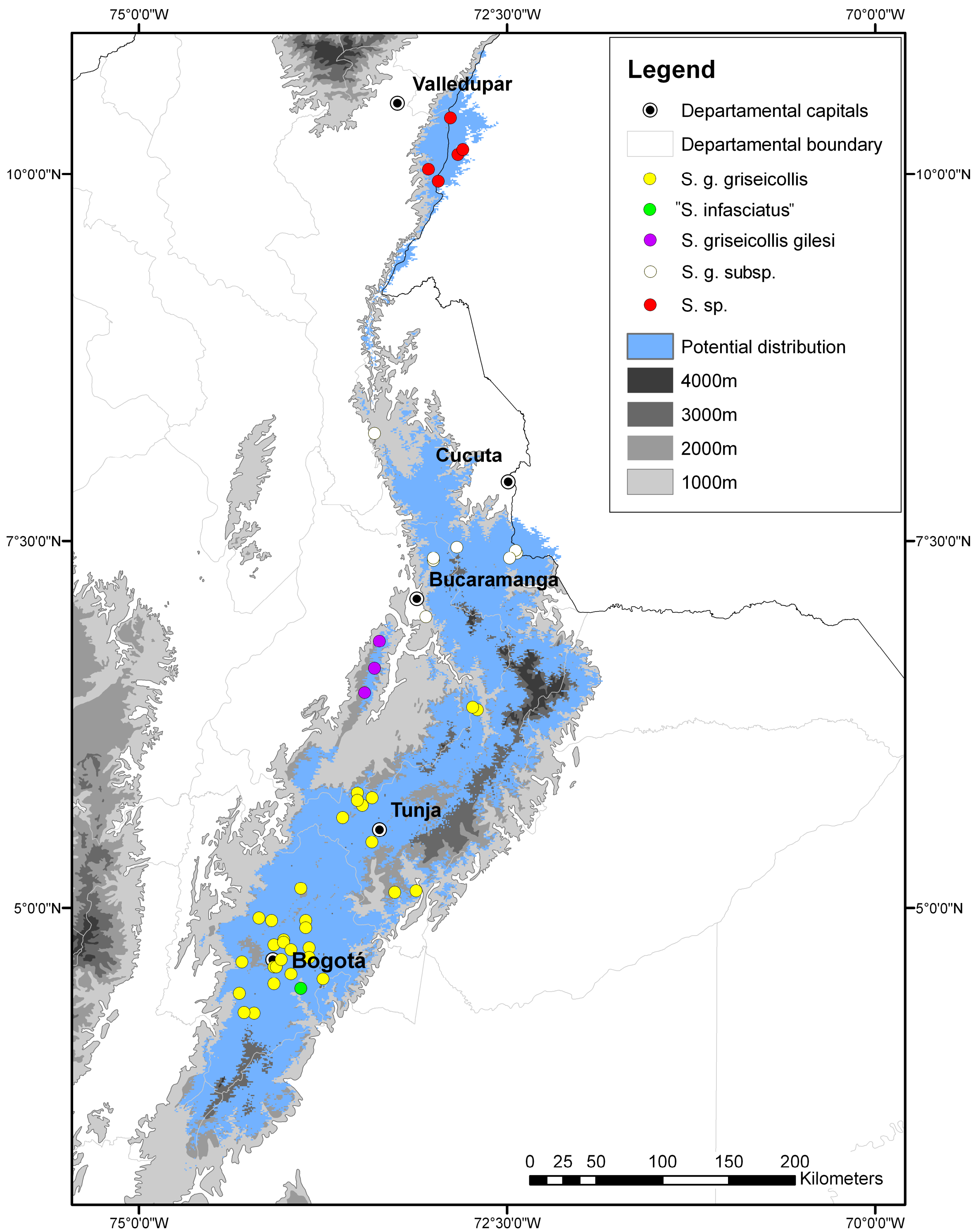

Figure 9: Potential distribution map by J. Velázquez using MAXENT 3.0 (Phillips et al. 2006) showing locations of records of *S. griseicollis* in the Eastern Andes Colombia, with potential distribution based on topography and climate layers available from Worldclim (Hijmans et al. 2005). Localities in Serranía de los Yariguíes are north to south: Alto Cantagallos; Filo Pamplona and Lepipuerto. Note the apparent isolation of the Yariguíes and Perijá populations; and lack of geographic barrier between "*S. infasciatus*" type locality and "*S. griseicollis*" sites.

rent slopes. It is absent from the more windswept páramo of highest elevations (which consists principally of stunted bromeliads and reeds) and from forest below the treeline. Based on our estimate of the area of páramo-forest ecotone at appropriate elevations for the species (IGAC 1995) and forest coverage information (IGAC 1999), there should be approximately 12.6km^2 of suitable habitat for *S. g. gilesi* (7.5 and 5.1km^2 on east and west slopes, respectively). It is abundant in such habitats, with an estimated density of 2.65 individuals/ha or 265 individuals/km^2 based on data from our fieldwork. Assuming 70-100% occupancy in suitable habitat produces a total estimated population of ca. 2300-3300 individuals. Despite its small range, *S. g. gilesi* would not qualify for Vulnerable under category D1 on a basis of its population alone, but could be considered Near-Threatened. It technically qualifies as Vulnerable under D2 on account of being recorded in less than three localities but habitat is fairly continuous in the Yariguíes range, meaning that there must be many other sites. The relative intactness of the remaining forest at high elevations in the Yariguíes suggests that the population is unlikely to be declining by >30% over ten years (criterion A), nor is the habitat is "severely fragmented" (required to qualify for criterion B). Deforestation continues in lowlands and foothill to premontane regions of the Yariguíes mountains, but the highest elevations remain remote.

In light of the inaccessibility of *S. g. gilesi*'s habitat, its high abundance where found, lack of hunting or trade threats for *Scytalopus* and the adaptability of *S. griseicollis* to secondary habitats, we are not particularly concerned for the long-term conservation of this taxon at present. We also note that the Serranía de los Yariguíes National Park was declared on 16 May 2005 (Ministerio del Medio Ambiente, Desarrollo y Vivienda 2005), following biological justification provided by our and other studies. NGOs have declared the region an Alliance for Zero Extinction site (Ricketts et al. 2005) and an Important Bird Area (Franco & Bravo 2005), and Fundación ProAves has established a nature reserve in the region (discussed further in Donegan & Huertas 2005; Huertas & Donegan 2006). If these areas receive effective protection, it will assure the survival of *S. g. gilesi* as well as a number of other species endemic to the Eastern Andes, since they include the largest remaining block of forest in this EBA (Stattersfield et al. 1998).

Other northern populations of or related to *S. griseicollis*

North-south variation in *S. griseicollis* is evident and requires further research. Recent sound recordings (e.g. Fig. 1) and various specimens (Appendix 1; Fig. 9) confirm the presence of *S. griseicollis* in Tamá National Park, on both Colombian and Venezuelan sides of the national border and other localities in Santander and Norte de Santander departments. This population has a notably browner back in adult plumage than any of the other populations. *S. g. griseicollis* juveniles also have a brown back, but of a rather different shade. This undescribed population also has on average higher frequency scolds (Level 1). Although no obvious isolating barrier exists between these populations and those to the south (Fig. 9), several other understory highland species include a diffe-rent subspecies in the Tamá-Santander region (e.g. *Atlapetes schistaceus*, *Henicorhina leucophrys*). This population will be described elsewhere with other coauthors. In any event, this population is not *S. infasciatus* because the *infasciatus* type does not have a brown back.

Various specimens, most labelled "*Scytalopus meridanus*", have been collected in the Serranía de Perijá (Appendix 1; Figs. 9 & 10). Although Krabbe & Schulenberg (2003) did not assign this population to any described taxon, Hilty (2003) and Salaman et al. (2007) treated it provisionally as related to *S. meridanus*. Plumage and biometrics suggest strongly that this population is related to either *S. meridanus* or *S. griseicollis* (Fig. 10). Although the Perijá population has been sound recorded (C. Sharpe in litt. 2007) and collected recently (Appendix 1), recordings were not available for this study such that we cannot make strong conclusions about its status. Perijá birds cluster closer with those from the Venezuelan Andes for biometrics (Fig. 8) and are differ from Eastern Andes specimens up to Level 1 (and, for southern populations, Level 2) in bill and wing length; and from the Yariguíes population in their shorter tail (Levels 1, 2, and 4). The Perijá population is isolated from nominate *S. griseicollis* populations and *S. meridanus* by the narrow, low-elevation section of the Andes in the Ocaña region which is a formidable barrier to high elevation fauna (Stattersfield et al. 1998). An undescribed *Scytalopus* taxon is clearly involved.

VENEZUELAN ANDES: THE STATUS OF *S. MERIDANUS* AND *S. FUSCICAUDA*

Recent authors recognise two light-plumaged *Scytalopus* in the Venezuelan Andes: Mérida Tapaculo *S. meridanus* Hellmayr, 1922 is found across much of the range; and Lara Tapaculo *S. (griseicollis) fuscicauda* Hellmayr, 1922 is found in Lara state and on the Trujillo state border (e.g. Krabbe & Schulenberg 1997, 2003; Hilty 2003). *Scytalopus fuscicauda* is generally described as a high elevation bird with at most only traces of barring on its lower underparts (Hellmayr 1922, Zimmer 1939, Krabbe & Schulenberg 2003, Hilty 2003). *S. meridanus* has been considered a species with more strongly barred lower 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). Krabbe & Schulenberg (2003) ranked *fuscicauda* as a species, concluding that it was unlikely to be related to *S. griseicollis*. However, they noted that *S. fuscicauda* might be synonymous with *S. meridanus* and recommended further studies. Remsen et al. (2008) followed this approach and also treated *S. fuscicauda* as a species. 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 color morphs exist within what is currently referred to as "*S. meridanus*" in the Venezuelan Andes (see below). However, as suspected by Krabbe & Schulenberg (2003), we will argue that *S. meridanus* and *S. fuscicauda* should be treated as conspecific.

The type of *S. meridanus* (AMNH-492377) is a gray *Scytalopus* with a strongly barred orange-rufous vent. The specimen label states that it was collected at 4000m elevation at La Culata in Mérida state (08°45'N; 71°05'W, per Paynter 1982). Another *S. meridanus* specimen from this locality is labelled as having been collected at 3000m (Appendix 1). The *S. fuscicauda* type was collected by Carriker at Páramo de Rosas, close to the Trujillo state border in Lara state (09°35'N, 70° 07'W, 3245 m, per Paynter 1982). It differs from the *S. meridanus* type in lacking strong barring on the vent (Hellymar 1922; Fjeldså & Krabbe 1990; Hilty 2003), although Zimmer (1939) discerned weak barring not visible from the photographs we inspected. Hellmayr (1922) provisionally included in *S. meridanus* some specimens from Santa Marta, southern Colombia and Peru whilst noting that such specimens might refer to other taxa (as is now known to be the case), as well as at least one specimen from SW Lara state (Anzoátegui, Lara: 09° 36'N 69°54'W, per Paynter 1982). One BMNH skin (1914.11.26.507) labelled "*S. fuscicauda*", indistinguishable from others labelled as this form at BMNH, lacks strong barring and was collected at La Culata, Mérida, the type locality of *S. meridanus*. Zimmer (1939) also included a specimen from Guamito, Trujillo, within *S. fuscicauda*.

Individual morphological variation within the *S. meridanus* series at COP and elsewhere is remarkable, and the *S. fuscicauda* type falls within the range of plumage in this series. Specimens with strong barring on the vent have been collected in Táchira, Mérida, and Trujillo states and over a wide range of elevations (2200-3300 m). Specimens without strong barring are less frequent in collections but are found in series from Mérida, Trujillo, and Lara (*S. fuscicauda* type) states, and over a similar range of elevations (2400-3300 m). Birds with intermediate barring are also found in all states, with no discontinuity in this plumage feature or clear sex differences. Strongly barred and less strongly barred or unbarred birds thus do not separate out according to sex, elevation, or distribution. Individuals from different states and elevations in Venezuela similarly show no diagnostic differences in biometrics. We were only able to inspect one specimen from Lara state, which falls within the range of measurements of *S. meridanus* in biometrics. We tested Zimmer (1939)'s tentative hypothesis of bill size differences between his five "*fuscicauda*" and other *S. meridanus*, but we found no significant (Level 1) differences in any measurement (d.f.=7), with sample means of measurements of Lara and Trujillo specimens differing from those of Mérida specimens by <0.5 mm.

S. meridanus has an unusually wide elevational range, with skins from 2200m to 4000m and observations in PN Yacambú in Lara state down to 1600 m (P. Boesman in litt. 2006). Such an elevational range is similar to that of *S. griseicollis* in the Eastern Andes – which is present from 2450 m in forest (Yariguíes) or 1300 m in secondary growth (recent sound recording by A. Hernández-J. in IBA La Judía, Santander) up to 3900m at Laguna de Chisacal, Cundinamarca. We segregated Mérida range biometric data at arbitrary mid-elevation points to test the hypothesis that *fuscicauda* and *meridanus* might be elevational replacements, but found no Level 1 or greater differences. It is unlikely that two morphometrically and vocally indistinguishable *Scytalopus* species would co-occur across such a broad elevational and geographical range: indeed, Krabbe & Schulenberg (1997) found sharp elevational or habitat replacements to be frequent in this genus. The only case of which we are aware of true sympatry in the genus in Colombia is between *S. spillmanni* and *S. latrans*, which are two species with rather different plumage, biometrics, and vocalizations.

For voice, as for *S. griseicollis* and *S. infasciatus*, we inspected various recordings and assigned them to either of "*S. fuscicauda*" or "*S. meridanus*" based on proximity to the relevant type locality. Recordings in Boesman (1999) suggest that most of the vocalizations given in Táchira, Mérida, Trujillo, and Lara states are indistinguishable, including the scold (represented by spectrograms 68/71 in Krabbe & Schulenberg 1997) and some call notes (e.g. spectrograms 69/72). Reeling songs, similar to spectrogram 70, have also been recorded throughout the Venezuelan Andes. There is considerable intrapopulation variation in song speed, with calls often including short gaps between groups of two, three, or more notes (cf. some calls of *S. parkeri*), rather than in long, uninterrupted sequences (cf. *S. griseicollis* and *S. spillmanni*). In Táchira, Mérida, and Trujillo states, reeling songs often have introductory notes which are longer in duration than notes comprising the reeling song, though in one recording there is no such introduction. The two recordings we have inspected of reeling songs from Lara state (presumably "*S. fuscicauda*") have shorter introductory notes (noted by P. Boesman in litt. 2006). However, considerable individual variation in introductory phrases to reeling songs is evident within *S. griseicollis* and *S. spillmanni*. A larger sample of *S. meridanus* and *S. fuscicauda* recordings would be needed to assess whether these differences are due to individual or geographical variation. Even if such differences in introductory notes were to be confirmed with a greater sample, variables of song speed and acoustic frequency overlap considerably between western and eastern recordings for reeling songs, not reaching Level 1 diagnosis, let alone Level 4/5 that would be required for species rank.

In conclusion, no morphometric, biogeographic, plumage, or vocal data support 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. 2008) 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 most conservative approach at present would be to treat it as a subspecies of *S. meridanus*. We suspect that the two taxa are synonyms but we decline to go so far, pending analysis of a greater sample of vocalizations from Lara state and other regions.

Scytalopus 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" or "line priority" (under ICZN Article 69A.10, which applies to the fixation of type species for genera, a broadly analogous situation, 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. Because *meridanus* is the name which has been assigned to *Scytalopus* occurring in most of the Venezuelan Andes in three recent landmark publications (Krabbe &

Figure 10: Photographs showing various populations labelled "*S. meridanus*" from Venezuela. From left to right: (i) *Scytalopus sp.* of Perijá: COP 72580, Perijá, Zulia, Venezuela, 3000m, 6 July 1974; male; (ii) *S. griseicollis* undescribed *subsp.* COP 11101, collected at Páramo 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 *Scytalopus* 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 at COP by B. Huertas.

Schulenberg 1997 and 2003 and Hilty 2003), we formally propose that *meridanus* be given precedence over *fuscicauda* in the event that the two are considered conspecific or synonymous (for the purposes of ICZN Article 24.2).

Taxonomic rank of *Scytalopus meridanus* and *S. griseicollis*

Due to morphological similarities, all populations of gray tapaculos occurring in the northern Colombian and Venezuelan Andes have formerly been treated as conspecific (Zimmer 1939). The scolds and reeling songs of *S. griseicollis* taxa and *S. meridanus* taxa (as redefined above) are diagnosable to Levels 1 through 5 (Appendix 4), whilst note shape is different (Fig. 2). *Scytalopus meridanus* reeling songs become slower over time, being delivered in groups of 2-7 notes with spaces between them (vs. uniform delivery, with gradual slowing over time but no gaps, in *S. griseicollis*). Introductory notes are of a different note shape to the "zz" sometimes found in *S. griseicollis* recordings. Vocal differences between *S. griseicollis* and *S. meridanus* exceed those between sympatric *S. griseicollis* and *S. spillmanni*, requiring species rank for each of them under the Helbig et al. (2002) and Remsen (2005) guidelines.

THE POPULATION OF *SCYTALOPUS SPILLMANNI* IN THE EASTERN ANDES OF COLOMBIA

As discussed in Donegan et al. (2007), Spillmann's Tapaculo *S. spillmanni* was recently found in the Eastern Andes for the first time. The population shows differences from other populations in darker plumage (Fig. 11), tarsus length, song speed and acoustic frequency. However, it does not meet the requirements of all modern subspecies concepts. A preliminary molecular study of various *S. spillmanni* specimens including the Eastern Andes population is being undertaken, but results were not available for this paper. The Eastern Andes population is described and discussed below but is not formally named.

Localities for the Eastern Andes population of *S. spillmanni* and its potential range are shown in Figure 12; a model of potential distribution constructed using MAXENT suggest this population may be isolated from more southern and western populations due to the low elevations of the Eastern Andes ridge line in the Serranía de los Picachos region or further south. Specimens we ascribe to this population on the basis of morphology include two recent

Figure 11. Dorsal and ventral photographs of (left to right) two *S. spillmanni* Eastern Andes population (ICN 35605 (male) and 35608 (female) (both collected by the authors, Finca Pamplona/La Aurora, vereda San Isidro, municipality of Galán, Serranía de los Yariguíes, Santander, Colombia, 06º38'N; 73º24'W, 2700 m); one *S. spillmanni* Central Andes: ICN-33166 (male, Risaralda, Reserva Ucumarí, la Pastora, 2450 m, collected by J.A. Mobley on 5 January 1996); five *S. spillmanni* Western Andes: ICN-35034 (male, Antioquia, Jardín, Vda. Meseria, 05°29'N, 75°54W, 2200 m, collected by N. Krabbe on 23 August 2004), ICN-35033 (female, as previous but 2300 m, 22 August 2004), ICN-35032 (male, as previous); ICN-35029 (Antioquia, Urrao, Páramo Frontino, 06°25'N, 70°04'W, 2600 m, collected by N. Krabbe on 16 August 2004), ICN-35026 (as previous, 3150 m, 14 August 2004). Photograph at ICN by TMD.

Yariguíes specimens we collected, two MLS specimens labelled "*S. latebricola meridanus*" (Fig. 11) from near Pamplona, Norte de Santander, and a BMNH "Bogotá" skin labelled "*Scytalopus sylvestris*" (see Appendix 1).

Various *Scytalopus* species including *S. spillmanni* were previously treated as conspecific with *S. latebricola* (Zimmer 1939), but *S. latebricola* is now considered a monotypic endemic of the Santa Marta mountains of Colombia (Krabbe & Schulenberg 1997), with *S. meridanus* endemic to the Venezuelan Andes (see above). The type locality of "*S. sylvestris*" (now not considered a valid taxon) is Pallaypampa, Peru (Chapman 1915), so the BMNH specimen appears to have been misidentified. By biometrics, the MLS and BMNH specimens all fall within the range of the Eastern Andes *S. spillmanni* population. In Donegan et al. (2007), the MLS and BMNH skins mentioned above were thought possibly to relate to *S. rodriguezi*, but JEAC recently collected several specimens of the Yariguíes population that is related to *S. rodriguezi*, which has enabled comparison and rejection of this hypothesis. Two other MLS skins from Pamplona labelled "*S. latebricola meridanus*" are of the undescribed Tamá subspecies of *S. griseicollis*.

Individuals of the Eastern Andes *S. spillmanni* population were observed, sound recorded, or captured at three montane forest sites in Serranía de los Yariguíes: La Aurora, Lepipuerto, and Alto Cantagallos (details above). Other sound recordings were made at Finca La Carbonera, Los Robles, La Aguadita, Fusagasugá, Cundinamarca (4°25'N, 74° 19'W, 2450-2550m) by O. Laverde and (probably, although, as it is a song, we cannot exclude the possibility that the recording is not an unusual recording of *S. griseicollis*) at Vereda Carrizal, Sisavita, Cucutilla, Norte de Santander by S. Córdoba-C. (IAVH BSA 8887, 07°26'20N, 72° 50'27W, 2380m). Birds tentatively identified as *S. spillmanni* have been reported based on field observations at Rogitama, Boyacá (05°47'N, 73°31'W) and Santuario de Fauna y Flora Iguaque, Boyacá (05º40'N, 73º27'W) (J. Zuluaga in litt. 2006). No other skins of the Eastern Andes *S. spillmanni* population were found in any of the collections inspected nor are any observations reported by the members of the network of Colombian bird observers (RNOACOL).

DIFFERENCES FROM OTHER POPULATIONS.– The Eastern Andes population is clearly referable to *S. spillmanni* due to its broadly similar morphology and voice. Although both Yariguíes specimens are in molt and lack various tail feathers, the position of the feathers is consistent with the birds each having 12 or more rectrices, which is typical for *S. spillmanni*, whereas other *Scytalopus* of the Eastern Andes have only 10 rectrices (Krabbe & Schulenberg 1997). The type of *S. spillmanni* is from Volcán Illiniza, on the Pichincha/Cotopaxi border on the western slope of Ecuador (Stresemann 1937) and shares broadly similar dark plumage to the Eastern Andes population.

The Eastern Andes population differs from populations in Ecuador in its shorter tarsus length (Levels 1 & 2) and from populations in Eastern Ecuador by its slower song speed (Level 1; marginally missing Level 2). Due to slowing of song speed over time in longer calls, some *S. spillmanni* recordings attain slower speeds not reflected in average song speed data: the above analysis is based on average song speeds. Reeling songs from Western Ecuador are higher on average in acoustic frequency than in Eastern Ecuador (Level 1), with the Eastern Andes population intermediate (Level 1 from both). No recordings of the Eastern Andes population inspected include elaborate introductory sequences to songs nor are any composed of downstrokes. Such features are also rare or reduced in Central Andes recordings, but both are found in western and eastern slope *S. spillmanni* populations in Ecuador, including downstrokes in 80% of flat reeling songs. The Eastern Andes population appears small-bodied compared to Ecuadorian populations (but Yariguíes specimens had appreciable subcutaneous fat). A comparison of photographs suggests that the Ecuadorian and Eastern Andes populations might not be diagnosable by plumage, but direct comparisons of series have not been possible.

The Eastern Andes population can be distinguished from populations of *S. spillmanni* in the Central Andes by the lower acoustic frequency of its reeling songs (Levels 1 & 2: Figs. 4 & 5) and scolds (Levels 1 & 2: Fig. 3). Although insufficient data

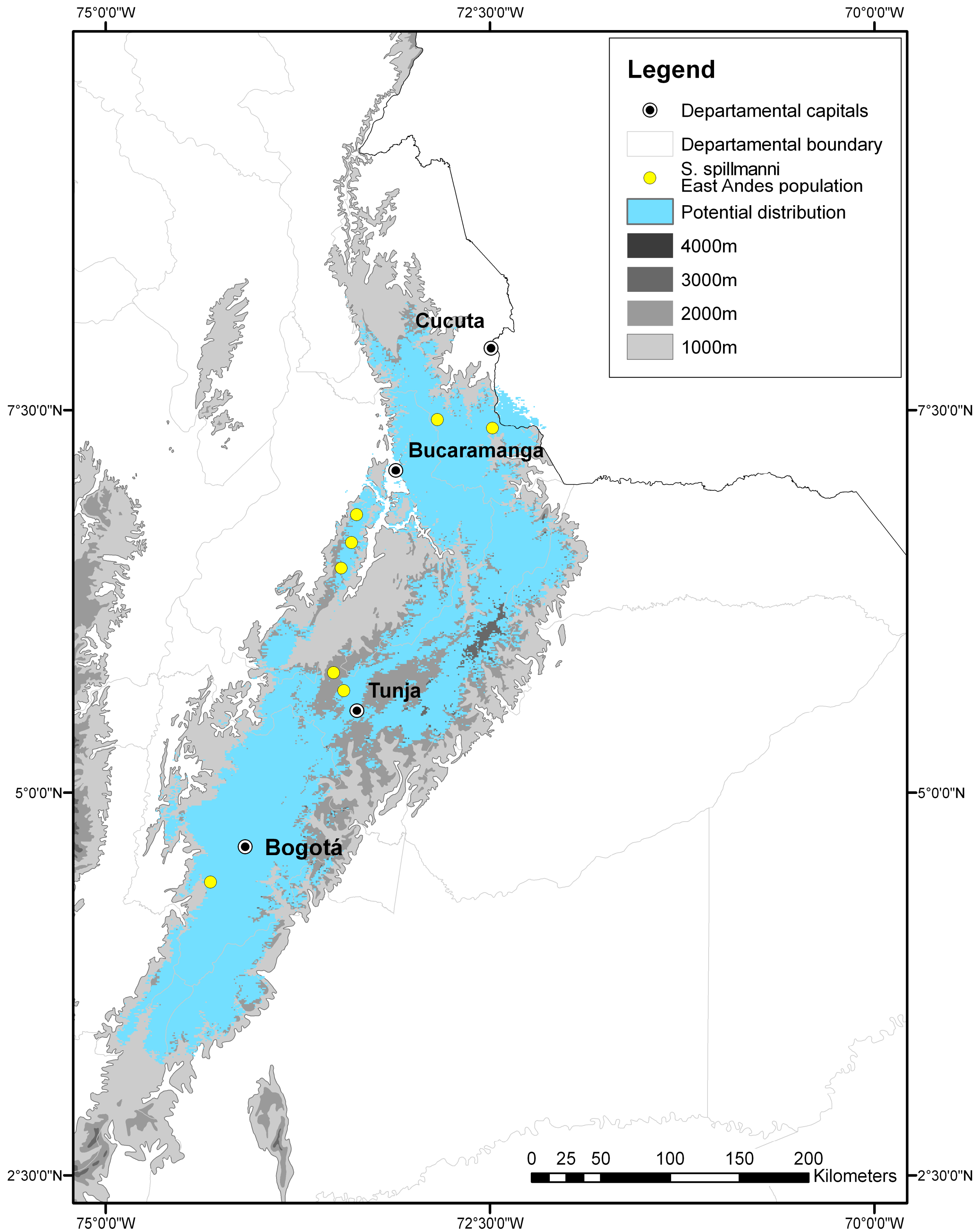

Figure 12. Potential distribution map by J. Velázquez using MAXENT 3.0 (Phillips et al. 2006) showing locations of records of *S. spillmanni* in the Eastern Andes Colombia, with potential distribution based on topography and climate layers available from Worldclim (Hijmans et al. 2005).

are available to assess biometrics, the two specimens we have measured of the Central Andes population are indistinguishable from Ecuadorian populations for tarsus length, tail length and mass, but fall outside the range of the Eastern Andes population. We have not considered in detail the status of Western Andes populations assigned to *S. spillmanni*, for which vocal differences from other *S. spillmanni* populations have been asserted (Krabbe et al. 2006). Our Yariguíes specimens are darker on the underparts and upperparts than recent Central and Western Andean specimens at ICN, although an old BMNH Central Andes skin is indistinguishable from the BMNH Eastern Andes skin.

An undescribed but well-known *Scytalopus* population in S Ecuador and Peru ("*S. cf. canus opacus*") has similar scolds to those of *S. spillmanni*. Such calls are diagnosably different from Ecuadorian populations of *S. spillmanni* but are not fully diagnosable from the Eastern Andes population (Fig. 3), leading to Donegan & Avendaño-C. (2006) erroneously referring to the population as "*Scytalopus sp nov (canus)*". Although scolds are very similar, the flat reeling songs of "*S. cf. canus opacus*" have a different note shape (essentially, a thick horizontal line), are of higher acoustic frequency than other populations and apparently have a different ratio between note duration and gap duration, whereas the female "brzk" call of "*S. cf. canus opacus*" bears little resemblance to that of *S. spillmanni*. Further research into this population and its affinities with *S. spillmanni* and true *S. canus opacus* is warranted. However, as this population differs diagnosably in its song from *S. spillmanni*, species rank with respect to *S. spillmanni* is not an issue. The similarity of scolds of *S. cf. canus opacus* and the Eastern Andes population of *S. spillmanni* begs further investigation.

It seems unlikely that the Eastern Andes population represents a point on a broad north-south cline of slowing song speed from populations in Ecuador. Comparison of vocal data between the 250 km distant Cundinamarca and Norte de Santander recordings of the Eastern Andes population (d.f.=4); and separately between Napo and Sucumbíos department populations on the east slope in Ecuador (d.f.=5) shows no statistically significant differences in song speed, with relatively high *t* (>0.5) values returned in each case and averages <0.7 notes/s different. The Tamá recording, if confirmed to be of *S. spillmanni*, would fall within the range of other Eastern Andes recordings for measured variables but specimens have lighter plumage than Yariguíes birds. East slope Ecuador recordings were slightly faster on average than west slope Ecuador recordings (but not to Level 1), meaning that the Eastern Andes population was marginally more distinct vocally from the geographically closer population (App. 4). Slower song speed appears to be a feature of populations in all three Colombian cordilleras, with the few Western Andes recordings we have inspected also having slower songs (as noted by Krabbe et al. 2006) . Though we lack vocal data from Nariño to Caquetá, it would be inconsistent with variation elsewhere for a broad cline to occur in this region. The single Central Andes Huila recording in our sample is a curtailed rising reeling song at 29.5 notes/s, suggesting that it is related to the Central Andes population (slower than 97% of the Ecuador population's songs; and curtailed songs typically are faster than elongated songs due to a lack of slowing over time more pronounced in longer songs). The differentiation of a slower (vs. Ecuador) and higher (vs. Central Andes) song in the Eastern Andes is notable given sympatry in this region with *S. griseicollis*, a species with a similar but faster-paced and lower frequency song. No such similarly-calling, apparently closely related, species are sympatric with *S. spillmanni* elsewhere in the northern Andes. Acoustic frequency appears to be more plastic than song speed in these *Scytalopus*. Variation in acoustic frequency between *S. griseicollis* populations is also evident. It is intriguing that the Eastern Andes population has higher frequency calls and the Central Andes population lower frequency calls, representing the reverse west-east pattern to that observed in Ecuador and again possibly influenced by *S. griseicollis*.

NOTES ON OTHER NORTHERN RHINOCRYPTIDAE

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 Eastern 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 at around 2000 m elevation in Serranía de los Yariguíes (see Donegan et al. 2007 and specimens listed in Appendix 1). This population is apparently not closely related to either *S. meridanus* or *S. griseicollis*, having darker plumage and a different voice. It has a longer tail (Levels 1,2 and 4, d.f.=2) than *S. rodriguezi*. Separately, four COP specimens collected at 2200-2400m elevation in the Venezuelan Andes (listed in Appendix 1) have a darker shade of gray plumage overall, a darker and browner shade of rufous on the underparts (which are all strongly barred: Fig. 11, plate of "*S. meridanus*" in Hilty 2003), and a longer tail than *S. meridanus* (Levels 1 & 2, d.f.=2). These specimens appear likely to be of an undescribed color morph or species (possibly related to *S. spillmanni, S. micropterus* or *S. rodriguezi*). These populations will be considered in further detail in future publications.

Blackish Tapaculo *S. latrans* is another widespread species of the northern Andes. Our specimen from La Aurora and others observed at the same site (but not others in the Yariguíes) had a pinkish white bill base, a feature not previously observed for the species and perhaps a local leucism. Central Andes specimens of *S. latrans*, including live and recently -collected specimens, are not as dark as West and Eastern Andes specimens. Although songs and some calls are similar to those of other populations, our recording of the "brzk" call of *S. latrans* in Serranía de los Yariguíes shows small differences from populations in Ecuador. Krabbe & Schulenberg (1997) reported differences in plumage between west and east slope populations of this species in Ecuador and recordings in Krabbe & Nilsson (2004) evidence geographic variation in voice in Ecuador. Intraspecific variation in *S. latrans* is a matter in great need of further research.

Other *Scytalopus* taxa present in the Eastern Andes include Long-tailed Tapaculo *S. micropterus,* which is present apparently on the east slope (Salaman et al. 2002) and replaced by *S. rodriguezi* at similar elevations on the west slope. The foothill species White-crowned Tapaculo *S. atratus* is also present on both slopes of the Eastern Andes (Donegan et al. 2007; Cuervo et al. 2007) and in the Venezuelan Andes. Finally. *S. caracae* is present in the Coastal Cordillera of Venezuela. A recent *Scytalopus* record in the Caripe mountains further to the east (Hilty 2003) requires urgent attention in light of the status of the region as a center of avian endemism and high threat levels (Stattersfield et al. 1998).

The monotypic Ash-colored Tapaculo *Myornis senilis* occurs at high elevation sites (mostly páramos) in Ecuador and all three Andean ranges of Colombia. Some variation in darkness of plumage and biometrics is evident among Colombian populations. As with *S. spillmanni*, Central Andes birds are similar morphometrically to those in Ecuador; whilst East Andes and West Andes birds show small differences. Whether such variation is of a similar nature to that in *S. spillmanni* or requires the description of new taxa is a matter requiring further investigation.

DISCUSSION

Allopatric populations in the process of speciation, which have reached a certain level of differentiation, are cases where subspecies rank is likely to be an appropriate taxonomic treatment. The recognition of isolated populations such as the East Andes population of *S. spillmanni* as subspecies would facilitate communication and draw attention to the differentiation of the population. On the other hand, populations showing only small average differences should not be recognized as subspecies. The various proposed subspecies tests considered in this paper each seek to balance these concerns.

Several antbird taxa have been ranked as valid subspecies on a basis of qualitatively diagnostic plumage characters but show only non-diagnostic, vocal differences from proposed conspecifics (Isler et al. 1998, 1999, 2006, 2007). For *Scytalopus*, plumage and biometrics are often not diagnostic even among species (Krabbe & Schulenberg 1997), and a diagnostic difference in a single vocal variable is regarded herein as sufficient for species rank. Various tapaculo species have allopatric populations that show some geographic variation in voice but no obvious plumage differences (e.g. *S. latrans*: Krabbe & Nilsson 2004; *S. atratus*: Cuervo et al.

2007; Donegan et al. 2007; *S. spillmanni*: this study). "Relatively minor or few diagnostic characters" (per the Isler et al. model for antbirds) may therefore be an illusive criterion for the ranking of subspecies within some *Scytalopus* species. *S. griseicollis gilesi* and the undescribed Tamá subspecies of *S. griseicollis* are rare cases of *Scytalopus* populations that have diagnostic plumage characters but which are not diagnosable by voice or biometrics. The Eastern Andes population of *S. spillmanni* shows similar differentiation of vocal and biometric characters as *S. griseicollis* subspecies, suggesting similar isolation, but is not capable of formal description under our conservative approach owing to the lack of a single diagnostic (plumage) character.

Our Level 1 test of statistical significance tolerates a considerable degree of overlap, meaning that, if it were used as a subspecies test, the placement of a particular individual with one taxon or another may be difficult; and "subspecies" may involve narrower distinctions, risking a destabilizing taxonomic inflation. Our Levels 1 and 2 involve a greater level of differentiation and reflect variation in vocal and biometric variables among 'good' *S. griseicollis* subspecies. However, the Hubbs & Perlmutter (1942) test is rarely used today in favor of the Amadon (1948) test, raising universality issues and risking taxonomic inflation.

The traditional Level 3 "99+%/75%" test for subspecies (Amadon 1948; Patten & Unitt 2002; Cicero & Johnson 2006) is an arbitrary one and has been criticized (e.g. Zink 2003). As noted by Amadon (1948), the 99+%/75% test is "roughly equivalent" to 97%/97% diagnosability – which (if repeated for multiple characters) is essentially the benchmark of current tests of species rank under biological species concepts (e.g. Isler et al. 1998). Under phylogenetic species concepts, two allopatric phylogenetic species would be recognized when, for a continuous variable with infinite sample size, sample means are 4.00 standard deviations apart (Level 4/5). The assessment of a subspecies where sample means are between 3.92 ($=t_{99.9\%@\infty} + t_{75\%@\infty}$) and 4.00 standard deviations ($=2t_{97.5\%@\infty}$) apart would result in very few populations (falling within a range of 0.08 standard deviations' difference for a continuous variable with infinite sample size) being ranked as subspecies under some approaches. A separate difficulty arises where smaller samples are involved, which is a hazard for comparative studies of some Neotropical bird populations. Where t values are used rather than recorded standard deviations, $t_{99.9\%}$ becomes increasingly large compared to $t_{97.5\%}$ with smaller samples. Where d.f.<8, Isler et al. (1998)'s diagnosability test for species (Level 5) may be met where the traditional subspecies test (Level 3) is not. Where 99%/75% diagnosability is used (as here), rather than 99.9%/75%, the availability of subspecies rank includes cases where sample means fall between 3.00 (rather than 3.92) and 4 standard deviations apart at infinity and the scope for 'species not being subspecies' is restricted to even smaller samples (d.f.<4), giving the concept of "subspecies" more meaning.

The East Andes population of *S. spillmanni* meets the Luckow (1995) "Level 1" test; and the Hubbs & Perlmutter (1942) Level 2 test for subspecies but fails all others based on our current data set: in summary, observed differences in voice and biometrics are statistically significant and sample means of at least one variable fall between 2 and 3 standard deviations apart (controlling for sample size). This is not sufficient for ranking of a subspecies under modern concepts. Biometrics of *S. spillmanni* populations should be re-evaluated once a greater sample size is available and we await the results of molecular studies with interest.

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LITERATURE CITED

ÁLVAREZ-R, M. & S. CÓRDOBA-C. 2002. Guía sonora de las aves del departamento de Caldas, cuencas de los ríos Tapias y Tareas. Serie CARs. Banco de Sonidos Animales (BSA). Instituto de Investigación de Recursos Biológicos Alexander von Humboldt. Villa de Leyva, Colombia.

ÁLVAREZ-R, M., V. CARO, O. LAVERDE & A. M. CUERVO. 2007. Guía sonora de los Andes colombianos. Instituto Alexander von Humboldt & Cornell Laboratory of Ornithology.

AMADON, D. 1949. The seventy-five per cent rule for subspecies. Condor 51:250-258.

ANÓNIMO. 2005. *Parque Nacional Natural Serranía de los Yariguíes. Documento de Declaratoria*. Ministerio del Medio Ambiente, Desarrollo y Vivienda, Bucaramanga, Colombia, May 2005.

ARCTANDER, P. & J. FJELDSÅ. 1994. Andean Tapaculos of the genus *Scytalopus* (Aves, Rhinocryptidae): a study of modes of differentiation using DNA sequence data. Pp. 205-225 in Conservation Genetics (V. Loeschke, J. Tomiuk, & S. K. Jain, Eds.) Birkhauser Verlag, Basel, Switzerland.

ASOCIACIÓN BOGOTANA DE ORNITOLOGÍA (ABO). 2000. Aves de la Sabana de Bogotá, guía de campo. ABO-CAR, Bogotá.

BORNSCHEIN, M. R., B. L. REINERT & M. PICHORIM. 1998. Descrição, ecologia e conservação de um novo *Scytalopus* (Rhinocryptidae) do sul do Brasil, com comentários sobre a morfologia da família. Ararajuba 6: 3-36.

BORNSCHEIN, M. R., G. N. MAURICIO, R. BELMONTE-LOPES, H. MATA & S. L. BONATTO. 2007. Diamantina Tapaculo, a new *Scytalopus* endemic to the Chapada Diamantina, northeast Brazil (Passeriformes: Rhinocryptidae). Revista Brasileira de Ornitologia 15:151-174.

BIRDLIFE INTERNATIONAL. 2004. Threatened birds of the world 2004. CD-ROM. BirdLife International, Cambridge, UK.

BIRDLIFE INTERNATIONAL. 2007. What's new (2007): species changing IUCN Red List. URL: http://www.birdlife.org/action/science/species/global_species_programme/whats_new.html

BOESMAN, P. 1999. Birds of Venezuela: photographs, sounds and distributions. CD-ROM. Bird Songs International.

CHAPMAN, F. M. 1915. The more northern species of the genus *Scytalopus* Gould. Auk 32:406-423.

COOPMANS, P., N. KRABBE & T. S. SCHULENBERG. 2001. Vocal evidence of species rank for nominate Unicolored Tapaculo *Scytalopus unicolor*. Bulletin of the British Ornithologists' Club 121:208-213.

CUERVO, A. M., F. G. STILES, C. D. CADENA, J. L. TORO & G. A. LONDOÑO. 2004. New and noteworthy records from the northern sector of the Western Andes of Colombia. Bulletin of the British Ornithologists' Club 123:7-24.

CUERVO, A. M., C. D. CADENA, N. KRABBE & L. M. RENJIFO. 2005. *Scytalopus stilesi*, a new species of tapaculo (Rhinocryptidae) from the Cordillera Central of Colombia. Auk 122(2): 445-463.

CUERVO, A. M., A. HERNÁNDEZ-J., J. O. CORTÉS-H. & O. LAVERDE. 2007. Nuevos registros de aves en la parte alta de la Serranía de las Quinchas, middle Magdalena valley, Colombia. Ornitología Colombiana 5: 94-98

DONEGAN, T. M. & B. C. HUERTAS (eds.) 2005. Threatened Species of Serranía de los Yariguíes: Final Report. 81 pp. Colombian EBA Project Report Series 5: www.proaves.org.

DONEGAN, T. M., B. C. HUERTAS & E. R. BRICEÑO. 2005. Discovery of a population stronghold of Gorgeted Wood-Quail *Odontophorus strophium*, a critically endangered Colombian endemic, with notes on ecology and vocalisations. Cotinga 23:74-77

DONEGAN, T. M., J. E. AVENDAÑO-C., E. R. BRICEÑO & B. C. HUERTAS. 2007. Range extensions, taxonomic and ecological notes from Serranía de los Yariguíes, Colombia's new National Park. Bulletin of the British Ornithologists' Club 127:172-213.

FJELDSÅ, J. & N. KRABBE. 1990. Birds of the high Andes. University of Copenhagen Zoological Museum and Apollo Books, Copenhagen.

FRANCO, A. M. & G. BRAVO. 2005. Áreas importantes para la conservación de las aves en Colombia. pp.117-281 in Boyla, K. & Estrada, A. (eds.) 2005. Áreas importantes para la conservación de las aves en los Andes tropicales. BirdLife Ecuador, Quito.

FUNDACIÓN NATURA. 2003. Caracterización social, económica institucional en forma participativa del eje central de conservación de la Serranía de los Yariguíes. Fundación Natura, Fonade, Ministerio del Medio Ambiente, CAS, UAESPNN, Gobernación de Santander & AMAY. CD-ROM.

HELBIG, A. J., A. G. KNOX, D. T. PARKIN, G. SANGSTER & M. COLLINSON. 2002. Guidelines for assigning species rank. Ibis 144:518-525.

HELLMAYR, C. E. 1922. Neue formen der gattung *Scytalopus*. Ornithologische Monatsberichte 30:54-59.

HILTY, S. L. 2003. Birds of Venezuela. Princeton University Press, Princeton, N. J.

HUBBS, C. L. & A. PERLMUTTER. 1942. Biometric comparison of several samples with particular reference to racial investigations. American Naturalist 76: 582-592.

HIJMANS, R. J., S. E. CAMERON, J. L. PARRA, P. G. JONES & A. JARVIS. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25:1965-1978.

HUERTAS, B. C. & J. J. ARIAS. 2007. A new butterfly species from the Colombian Andes and a review of the taxonomy of the genera *Idioneurula* Strand, 1932 and *Tamania* Pyrcz, 1995 (Lepidoptera: Nymphalidae: Satyrinae). *Zootaxa* in press.

HUERTAS, B. C. & T. M. DONEGAN (eds.) 2006. Proyecto YARÉ: Investigación y Evaluación de las Especies Amenazadas de la Serranía de los Yariguíes, Santander, Colombia. BP Conservation Programme. Informe Final. Colombian EBA Project Report Series 7: www.proaves.org

IGAC (INSTITUTO GEOGRÁFICO AGUSTIN CODAZZI). 1995. Unnamed countour maps, nos. 120, 135, 150 & 151. IGAC, Colombia.

IGAC (INSTITUTO GEOGRÁFICO AGUSTIN CODAZZI). 1999. Espaciomapas nos. 120 & 135. IGAC, Bogotá.

ISLER, M. L., P. R. ISLER & B. M. WHITNEY. 1998. Use of vocalizations to establish species limits in antbirds (Passeriformes; Thamnophilidae). Auk 115:577-590.

ISLER, M. L., P. R. ISLER & B. M. WHITNEY. 1999. Species limits in Antbirds. The *Myrmotherula surinamensis* complex. Wilson Bull. 116:83-96.

ISLER, M. L., P. R. ISLER & B. M. WHITNEY. 2006. Species limits in Antbirds (Thamnophilidae): the Warbling Antbird (*Hypocnemis cantator*) complex. Auk 124:11-28.

ISLER, M. L., P. R. ISLER & B. M. WHITNEY. 2007. Species limits in the "*Schistocichla*" complex of *Percnostola* antbirds (Passeriformes: Thamnophilidae). Wilson Journal of Ornithology 119:53 -70.

ISLER, M. L., P. R. ISLER & B. M. WHITNEY. 2008. Species limits in antbirds (Aves: Passeriformes: Thamnophilidae): an evaulation of Plumbeous Antvireo *Dysithamnus plumbeus* based on vocalizations. Zootaxa 1726: 60-68.

KRABBE, N., J. V. MOORE, P. COOPMANS, M. LYSINGER & R. S. RIDGELY. 2001. Birds of the Ecuadorian highlands: the upper montane and páramo zones of Ecuador. CDs. John V. Moore Nature Recordings, San José, CA.

KRABBE, N., P. SALAMAN, A. CORTÉS, A. QUEVEDO, L. A. ORTEGA & C. D. CADENA. 2005. A new species of *Scytalopus* tapaculo from the upper Magdalena Valley, Colombia. Bulletin of the British Ornithologists' Club 125:93–108.

KRABBE, N., P. FLÓREZ, G. SUÁREZ, J. CASTAÑO, J. D. ARANGO & A. DUQUE. 2006. The birds of Páramo Frontino, West Andes of Colombia. Ornitología Colombiana 4:39–50.

KRABBE, N. & J. NILSSON. 2004. Birds of Ecuador: sounds and photographs. DVD ROM. Bird Songs International, Netherlands.

KRABBE, N. & T. S. SCHULENBERG. 1997. Species limits and natural history of *Scytalopus* tapaculos (Rhinocryptidae), with descriptions of the Ecuadorian taxa, including three new species. Pp. 47-88 in: Studies in Neotropical Ornithology Honoring Ted Parker (J.V. Remsen, Jr., ed.) Ornithologial Monographs, no. 48.

KRABBE, N. & T. S. SCHULENBERG. 2003. Family Rhinocryptidae (tapaculos). Pp. 748-787 in Handbook of the Birds of the World, vol. 8: Broadbills to Tapaculos (J. del Hoyo, A. Elliot, and D. Christie, Eds.). Lynx Edicions, Barcelona, Spain.

KROODSMA, D. E. 1984. Songs of the Alder Flycatcher (*Empidonax alnorum*) and Willow Flycatcher (*Empidonax traillii*) are innate. Auk 101: 13-24.

LUCKOW, M. 1995. Species concepts: assumptions, methods, and applications. Systematic Botany 20:589-605.

MAURICIO, G. N. 2005. Taxonomy of southern populations in the *Scytalopus speluncae* group, with description of a new species and remarks on the systematics and biogeography of the complex (Passeriformes: Rhinocryptidae). Ararajuba 13:7-28.

MUNSELL COLOR. 1977. Munsell® color charts for plant tissues. GretagMacbeth LLC, New York.

MUNSELL COLOR. 2000. Munsell® soil color charts. GretagMacbeth LLC, New York.

ORME, C. D. L., R. G. DAVIES, M. BURGESS, F. EIGENBROD, N. PICKUP, V. A. OLSON, A. J. WEBSTER, T-S. DING, P. C. RASMUSSEN, R. S. RIDGELY, A. J. STATTERSFIELD, P. M. BENNETT, T. M. BLACKBURN, K. J. GASTON & I. P. F. OWENS. 2005. Global hotspots of species richness are not congruent with endemism or threat. Nature 436: 1016 – 1019.

PATTEN, M. A. & P. UNITT. 2002. Diagnosability versus mean differences of Sage Sparrows subspecies. Auk 119: 26-35.

PAYNTER, R. A. JR. 1982. Ornithological gazetteer of Venezuela. Museum of Comparative Zoology, Cambridge, MA.

PAYNTER, R. A. JR. 1997. Ornithological gazetteer of Colombia, 2nd ed. Harvard University. Cambridge, M. A.

PETERS, J. L. 1951. Check-list of birds of the world, vol. 7. Museum of Comparative Zoology, Cambridge, MA.

PETERSON, A. T. & A. G. NAVARRO-SIGUENZA. 1999. Alternate species concepts as bases for determining priority conservation areas. Conservation Biology 13:427-431.

PHILLIPS, S. J., R. P. ANDERSON & R. E. SCHAPIRE. 2006. Maximum entropy modelling of species geographic distributions. Ecological Modelling 190:231–259.

PHILLIMORE, A. B., C. D. L. ORME, R. G. DAVIES, J. D. HADFIELD, W. J. REED, K. J. GASTON, R. P. FRECKLETON & I. P. F. OWENS. 2007. Biogeographical basis of recent phenotypic divergence among birds: a global study of subspecies richness. Evolution 61:942-957.

PULGARÍN-R, P. C. 2007. El nido y los huevos del Tapaculo de Spillmann (*Scytalopus spillmanni*). Ornitología Colombiana 5:91-93.

RAPOSO, M. A., R. STOPIGLIA, V. LOSKOT & G.M. KIRWAN. 2006. The correct use of the name *Scytalopus speluncae* (Ménétriés, 1835) and the description of a new species of Brazilian tapaculo (Aves: Passeriformes: Rhinocryptidae). Zootaxa 1271:37-56.

RESTALL, R., C. RODNER & M. LENTINO. 2006. Birds of Northern South America: an identification guide. Helm Field Guides.

REMSEN, J. V., JR. 2005. Pattern, process, and rigor meet classification. Auk 122: 403-413.

REMSEN, J. V., C. D. CADENA, A. JARAMILLO, M. NORES, J. F. PACHECO, M. B. ROBBINS, T. S. SCHULENBERG, F. G. STILES, D. F. STOTZ & K. J. ZIMMER. 2008. A classification of the bird species of South America (version 4 March 2008). American Ornithologists' Union. URL: http://www.museum.lsu.edu/~Remsen/SACCBaseline.html

RICKETTS, T.H., E. DINERSTEIN, T. BOUCHER, T. M. BROOKS, S. H. B BUTCHART, M. HOFFMANN, J. LAMOREUX, J. MORRISON, M. PARR, J. D. PILGRIM, A. S. L. RODRIGUES, W. SECHREST, G. E. WALLACE, K. BERLIN, J. BIELBY, N. D. BURGESS, D. R. CHURCH, N. COX, D. KNOX, C. LOUCKS, G. W. LUCK, L. L. MASTER, R. MOORE, R. NAIDOO, R. RIDGELY, G. E. SCHATZ, G. SHIRE, H. STRAND, W. WETTENGEL & E. WIKRAMANAYAKE. 2005. Pinpointing and preventing imminent extinctions. Proceedings of the National Academy of Sciences 51: 18497-18501.

RIDGELY, R. S. & G. TUDOR. 1994. The Birds of South America: Vol. 2, the Suboscine Passerines. Oxford University Press, Oxford, UK.

RIDGWAY, R. 1911. The birds of North and Middle America, part V. Bulletin of the United States National Museum, no. 50.

SALAMAN, P. G. W., F. G. STILES, C. I. BOHÓRQUEZ, M. ÁLVAREZ-R, A. M. UMAÑA, T. M. DONEGAN & A. M. CUERVO. 2002. New and noteworthy records from the east slope of the Andes of Colombia. Caldasia 24:157-189.

SALAMAN, P.G.W, DONEGAN, T.M. & CARO, D. 2007. Lista de Chequeo de las Aves de Colombia. *Conservación Colombiana* 2 Suplemento. 85 pp. Fundación ProAves, Bogotá, Colombia.

STATTERSFIELD, A. J., M. J. CROSBY, A. J. LONG, & D. C. WEGE. 1998. Endemic Bird Areas of the World: Priorities for Biodiversity Conservation. BirdLife International, Cambridge: BirdLife Conservation Series 7.

STILES, F.G. & P. CAYCEDO. 2002. A new subspecies of Apolinar's Wren (*Cistothorus apolinari*, Aves: Troglodytidae), an endangered Colombian endemic. Caldasia 24:191-199.

STRESEMANN, E. 1937. Vögel von Monte Illiniza (Central-Ecuador). Ornithologische Monatsberichte 45:75-77.

SVENSSON, L. 1992. Identification guide to European passerines, 2nd ed. Published by author, Stockholm, Sweden.

WHITNEY, B. M. 1994. A new *Scytalopus* tapaculo (Rhinocryptidae) from Bolivia, with notes on other Bolivian members of the genus and the *magellanicus* complex. Wilson Bulletin 106:585-614.

ZIMMER, J. T. 1939. Studies of Peruvian Birds, No. 32. American Museum Novitates, No. 1044.

ZINK, R. M. 2003. The role of subspecies in obscuring avian biological diversity and misleading conservation policy. Proceedings of the Royal Society of London B. 27:561-564.

ZINK, R. M. 2005. Rigor and Species Concepts. Auk 122: 887-891.

ZINK, R.M. & J. V. Remsen, Jr. 1986. Evolutionary processes and patterns of geographic variation in birds. Current Ornithology 4: 1-69.

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APPENDIX 1: SPECIMENS EXAMINED All specimen localities are in Colombia unless otherwise stated.

Myornis senilis Ecuador: AMNH 186368, 492365, 173001, 492364, 124376, 180947, 180948, 184748, 39575 (all, Ecuador, no details taken); BMNH 1916.8.24.58 (Baeza, 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). Western Andes: ICN 35024, 35027 (both, Frontino, Urrao, Antioquia). Central Andes: AMNH 11851 (Laguneta, Quindio); ICN 26257 (Páez, PNN Nevado del Huila, Cauca). Eastern Andes: ANMH 121829 (El Peñon, Cundinamarca); AMNH 492366, 492367 (both, "Colombia"); 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"); ICN 12002-12006 (all San Miguel, Cundinamarca); MLS 3984 (PNN Chingaza, Boyacá), 3986 (San Miguel, Sibaté, 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 ("Bogotá"), 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 Páez, 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, Güayabetal, Cundinamarca, 2050m), 31788 (Cuchillas de Santa Bárbara, 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), 35607 (La Aurora, Galán, Serranía de los Yariguíes, 2750m; sound recording), 36177 (El Talismán, Serranía de los Yariguíes, Santander, 2100m), unnumbered (2) (La Lana, San Pedro de los Milagros, Antioquia, Colombia, 2700 m; sound recording); 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"); AMNH series inspected, no details taken.

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 Igüana, Serranía de los Churumbelos, Cauca); MNHN 1391 (E. Ecuador), 1933 (Alucincho, Ecuador); AMNH series inspected, no data taken.

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, Serranía de Aguas Claras, Cubarral, Meta), 34387 (Anorí, Antioquia), 35613 (Alto Honduras, Serranía de los Yariguíes, Santander, 1600m; sound recording); MNHN 386 (no data); AMNH series inspected, no data taken.

S. panamensis: BMNH 1921.7.3.69 (Tacarcuna, Panama); AMNH series inspected, no data taken.

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: ICN 35821 (La Luchata, Galán, Serranía de los Yariguíes, 2000m) 36178, 36179 (both, El Talismán, San Vicente de Chucurí, Serranía de los Yariguíes, 2100m; sound recording).

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

S. vicinior: ICN 31207, 31208 (both, 8km NE of Jeguadas, Alto de Pisones, Mistrató, Risaralda), 34840 (finca La Minga, vereda Chicoral, Cato Bitaco, La Cumbre, Valle); AMNH series inspected, no data taken.

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

S. meridanus (all Venezuela): AMNH 492377 (La Culata, Mérida, 4000m: type), rest of series inspected but no data taken; 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 (Güamito, Trujillo), 45378 to 45384 (all, Páramo Aricagüa, El Muerto, Falda Norte, Mérida, 3000-3140m), 49294 to 49298 (Santo Domingo, Mérida, 2300-2700m), 64259 to 64272 (Páramo La Negra, Mérida, 3200-3250m), 65206 (Güaraque, 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), 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 (Güamito, Trujillo); CM 37221 (type Páramo de Rosas, Lara), .

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 Ávila; Plan de Los Lirios, San Isidro, Distrito Federal, 1600-1700m), 13152 to 13155, 58455 to 58458, 61642 to 61643 (Caracas, León, Distrito Federal, 2000-2100m), 18850 to 18852 (all, Güarenas, Hacienda Izcaragüa, Miranda, 1400-1880m), 62603 to 62614 (all, Cerro el Ávila, San Isidro, Distrito Federal, 2000m), 62615 to 62617 (both, Cerro el Ávila, San Antonio de Galipán, Distrito Federal, 1600m), 62618 (Cerro el Ávila, Estación Teleférico, Distrito Federal, 2100m), 62619 to 62621 (Cerro el Ávila, Cerro Papelón, Distrito Federal, 1850-1900m), 75775 and 78732 (both, Colonia Tovar; Fundo Jeremba, Aragüa, 2300m).

Scytalopus spillmanni Ecuador and southern Colombian Andes: AMNH 176050 (Baeza, Ecuador), 180944 (Tambillo, Río Upano, Ecuador, 8000 ft.); (BMNH 1902.3.13.1261 (Porvenir, Bolívar, Ecuador); MFNU 1937.11.76 (type: Volcán Iliniza, Pichincha / Cotopaxi, Ecuador) (photographs); ANSP 8374, 8442, 8448, 8540 (all, Buena Vista, Huila, Colombia, 2300 m), 176867, 176868, 176869, 176870, 176871, 176872 (all, west slope Andes, road from Quito to Mindo, 2.5 km south of Tandayapa, Pichincha, Ecuador, 2300 m), 178099, 178101, 178102 (all, SW slope of Volcán Pichincha, new road to Mindo, Pichincha, Ecuador, 2100m), 178100 (as previous, 2300 m), 181226, 181228 (both, west slope near road between Maldonado and Tulcán, along Río La Plata, Carchí, Ecuador, 2525 m, 0°48'N, 78°02'W) (photographs); FMNH 292133 (both, La Victoria, Nariño, Colombia, 2700m) 292135, 292138 (both, as previous, 2800m), 292139 (Llorente, Nariño, 1800m) (photographs). Western Andes: ICN 35026, 35029 (both, Páramo Frontino, Antioquia, 2600m), 35032, 35033, 35034 (all, vereda Meseria, Jardín, Antioquia, 2300m). Central Andes population: BMNH 1921.12.29.189 (La Guneta, Quindio, 10,300ft.); ICN 33166 (Ucumarí, Risaralda). Eastern Andes: BMNH 89.9-10.995 ("Bogotá"); ICN 35605 (male) and 35608 (female) (Finca Pamplona/La Aurora, vereda San Isidro, municipality of Galán, Serranía de los Yariguíes, Santander, Colombia, 06º38'N; 73º24'W, 2700 m; sound recording: tissue samples (heart) and skeleton at Universidad de los Andes); MLS 3990 (Fontibón, Pamplona, Norte de Santander, Colombia), 3991, (Alturas de Pamplona, Norte de Santander, Colombia).

S. sp. (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. g. griseicollis (including specimens labelled "*S. infasciatus*"): AMNH 132328 (type of *S. infasciatus*: Páramo de Beltrán) and rest of series inspected, no data taken; 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"); 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, Güasca, PNN Chingaza, Cundinamarca); ICN 10852 (vereda Ruparita, 2km E of Arcabuco, Boyacá), 10853 (vereda Puente Boyacá, Ventaquemala, Boyacá), 11982 to 11984 (all, Páramo de Güasca, Cundinamarca, 3500m), 11985 to 11988 (all, Alto Onzaga, Soatá, Boyacá), 12001 (Güasca, 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, Páramo de Guasca, Cundinamarca) 13015 to 13017 (Páramo de Palacio, Cundinamarca), 14074 (hacienda El Otoño, Sabana de Bogotá, Cundinamarca), 19963 (Monserrate, Bogotá, Cundinamarca), 24920 (Boquerón de Juan Viejo, Pasca, Cundinamarca), 31235, 31236 (both, Páramo 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), 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 undescribed Santander-Tamá subspecies: COP 11101 to 11103 (all, PNN Tamá, Apure, Venezuela 2800m), 62227 to 62229, 62231, 62244, 62245 (Río Chiquito, Hacienda La Providencia, Táchira, 2180-2300m), 73946 to 73952 (La Revancha, Cumbre, Cerro El Retiro, Táchira, 2700-2800m)); 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 36121 (Suratá, Santander), ICN 36416 (Piedecuesta, Santander); MLS 3992 (Alturas de Pamplona), 3993 (Fontibón, Pamplona).

S. griseicollis gilesi: ICN 35609 (sound recording), 35610, 36175 (details of each in text above).

S. sp. 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, Manaure, Serranía de Perijá, Cesar, Colombia, 2600m).

S. canus canus: AMNH series inspected, no data taken; BMNH 1921.7.3.70 (Paramillo, Antioquia, 12,500 ft); ICN 35020 (Páramo Frontino, Urrao, Antioquia, 3500m).

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

APPENDIX 2: BIOMETRICS OF NORTHERN RHINOCRYPTIDAE

In the table below, all data are from Colombia and Venezuela, with species marked * also including data from NHM and MNMH specimens from Ecuador. For each species’ measurement, data are presented as follows: mean ± standard deviation (minimum-maximum) (n= number of specimens). Species order and nomenclature follows Remsen et al. (2008), as modified herein.

Taxon	Wing chord from skins (mm)	Tail (mm)	Tarsus (mm)	Full culmen (mm)	Body mass (g)
*Myornis senilis**	57.5 ± 2.5 (55.0 -65.0) (n=28)	58.8 ± 4.2 (53.0 -63.0) (n=28)	21.9 ± 0.7 (21.0 -24.0) (n=28)	15.7 ± 0.9 (14.0 -17.5) (n=24)	19.0 ± 0.7 (18.5 -19.5) (n=2)
M. senilis Ecuador	59.4 ± 3.0 (55.0 -65.0) (n=9)	59.1 ± 2.3 (56.0 -63.0) (n=10)	22.1 ± 0.8 (21.0-24.0) (n=10)	15.9 ± 1.1 (14.0 -17.5) (n=9)	/
M. senilis W Andes	56.0 ± 0.0 (56.0 -56.0) (n=2)	68.5 ± 0.7 (68.0 -69.0) (n=2)	22.0 ± 0.0 (22.0 -22.0) (n=2)	16.8 ± 0.4 (16.5 -17.0) (n=2)	19.0 ± 0.7 (18.5 -19.5) (n=2)
M. senilis C Andes	59.0 ± 1.4 (58.0 -60.0) (n=2)	59.5 ± 4.9 (56.0 -63.0) (n=2)	21.5 ± 0.7 (21.0-22.0) (n=2)	/	/
M. senilis E Andes	56.4 ± 1.6 (54.0 -60.0) (n=15)	57.1 ± 3.6 (52.0 -63.0) (n=14)	21.8 ± 0.6 (21.0 -23.0) (n=14)	15.4 ± 0.6 (14.5 -16.5) (n=13)	/
*Scytalopus latrans**	56.0 ± 2.7 (52.0-60.0) (n=48)	39.6 ± 2.2 (35.0 -43.0) (n=43)	22.5 ± 0.9 (21.0-24.0) (n=45)	13.6 ± 0.9 (12.0-14.5) (n=45)	18.1 ± 1.7 (16.0-21.0) (n=12)
S. latrans W Andes	54.0 ± 2.2 (52.0 -57.0) (n=4)	39.3 ± 1.7 (37.0 -41.0) (n=4)	22.3 ± 0.5 (22.0-23.0) (n=4)	12.8 ± 1.1 (12.0-13.5) (n=2)	/

Taxon	**Wing chord from skins (mm)**	**Tail (mm)**	**Tarsus (mm)**	**Full culmen (mm)**	**Body mass (g)**
S. latrans C Andes	57.5 ± 2.5 (53.0 -60.0) (n=9)	38.6 ± 2.0 (36.0 -41.5) (n=9)	22.7 ± 0.9 (21.0-24.0) (n=10)	13.7 ± 0.6 (12.0-14.5) (n=10)	19.4 ± 1.5 (18.0 -21.0) (n=3)
S. latrans E Andes	55.0 ± 2.1 (52.0 -60.0) (n=28)	39.7 ± 2.2(36.0-43.0) (n=25)	22.4 ± 0.9(21.0 -24.0) (n=27)	13.4 ± 0.6 (12.0-14.5) (n=27)	17.4 ± 1.7 (16.0 -19.3) (n=7)
*S. micropterus**	59.2 ± 2.9 (55.0 -61.0) (n=6)	49.6 ± 4.8 (44.0 -56.0) (n=5)	24.5 ± 1.1 (23.0 -26.0) (n=5)	16.0 ± 0.7 (15.0 -16.5) (n=4)	/
S. atratus (nominate and *S. a. confusus*)	57.0 ± 1.4 (55.0 -59.0) (n=6)	40.0 ± 2.6 (36.0 -43.0) (d.f.=6)	22.5 ± 0.9 (21.0 -23.5) (n=6)	14.6 ± 0.6(14.0-15.5) (n=6)	/
S. panamensis	51 (n=1)	39 (n=1)	/	14.5 (n=1)	/
S. rodriguezi	54.3 ± 2.1 (52.0 -56.0) (n=3)	47.0 ± 1.7 (45.0 -48.0) (n=3)	22.5 ± 0.9 (22.0 -23.5) (n=3)	14.8 ± 0.3 (14.5 -15.0) (n=3)	21.5 ± 0.1 (21.4 -21.6) (n=3)
S.rodriguezi sp. (E. Andes: Col.)	55.7 ± 1.7 (52.0 -57.0) (n=7)	39.2 ± 1.8 (36.0 -40.2) (n=5)	20.8 ± 0.5 (20.0 -21.5) (n=5)	14.1 ± 0.4 (13.5 -15.0) (n=3)	17.1 ± 1.7 (15.1 -19.0) (n=4)
S. sp. (Ven. Andes)	53.0 ± 1.8 (51.0 -54.0) (n=4)	42.7 ± 0.6 (42.0 -43.0) (n=3)	22.4 ± 0.9 (21.5 -23.5) (n=4)	13.3 ± 0.3 (13.0 -13.5) (n=3)	/
S. stilesi	56.5 ± 0.8 (55.0 -57.0) (n=6)	43.3 ± 1.4 (41.0 -45.0) (n=6)	22.8 ± 0.6 (22.5 -24.0) (n=7)	15.1 ± 0.5 (14.5 -16.0) (n=6)	21.3 ± 0.8 (20.0 -22.0) (n=6)
S. vicinior	57.0 ± 1.7 (56.0-59.0) (n=3)	46.0 ± 2.6 (43.0 -48.0) (n=3)	22.7 ± 0.8(22.0-23.5) (n=3)	14.7 ± 0.3 (14.5 -15.0) (n=3)	24.2 ± 2.6 (21.5 -26.7) (n=3)
S. latebricola	58 (n=1)	36 (n=1)	23.0 (n=1)	14.0 (n=1)	/
S. caracae	52.8 ± 1.6 (50.0 -54.0) (n=5)	39.8 ± 1.9 (37.0 -42.0) (n=5)	21.9 ± 0.7 (21.0 -23.0) (n=5)	14.5 ± 0.5 (14.0 -15.0) (n=5)	/
Scytalopus spillmanni (E Andes) All	60.0 ± 2.9 (58.0 -65.0) (n=5)	39.4 ± 3.4 (36.0 -45.0) (n=5)	22.5 ± 0.5 (22.0 -23.0) (n=5)	13.2 ± 1.1 (11.5 -14.5) (n=5)	21.7 ± 1.8 (20.4 -23.0) (n=2)
Scytalopus spillmanni (E Andes) Males	60.7 ± 3.8 (58.0 -65.0) (n=3)	40.0 ± 4.6 (36.0 -45.0) (n=3)	22.8 ± 0.3 (22.5 -23.0) (n=3)	13.0 ± 1.5 (11.5 -14.5) (n=3)	23.0 (n=1)
Scytalopus spillmanni (E Andes) Fema-les	58.0 (n=1)	39.0 (n=1)	22.0 (n=1)	13.5 (n=1)	21.7 (n=1)
Scytalopus spillmanni Ecua-dor All	61.8 ± 2.4 (57.0 -67.0) (n=43)	45.2 ± 3.0 (39.0 -54.0) (n=39)	24.4 ± 1.0 (22.2 -26.0) (n=21)	14.5 (n=1)	25.1 ± 2.2 (20.5 -30.0) (n=43)
Scytalopus spillmanni Ecua-dor Males	62.2 ± 2.2 (58.0 -67.0) (n=37)	45.5 ± 3.1 (39.0 -54.0) (n=33)	24.5 ± 1.0 (22.2 -26.0) (n=18)	/	25.1 (20.5-30.0) (n=37)
Scytalopus spillmanni Ecua-dor Females	58.7 ± 1.5 (57.0 -60.0) (n=4)	43.0 (41.0-45.0) (n=4)	23.8 (23.5-24.1) (n=4)	/	24.9 (22.0-29.5) (n=5)
Scytalopus spillmanni (C Andes) Males	59.0 ± 1.4 (58.0 -60.0) (n=2)	41.5 ± 2.1 (40.0 -43.0) (n=2)	24.5 ± 0.7 (24.0 -25.0) (n=2)	15.0 ± 0.7 (14.5 -15.5) (n=2)	27.0 (n=1)

Taxon	**Wing chord from skins (mm)**	**Tail (mm)**	**Tarsus (mm)**	**Full culmen (mm)**	**Body mass (g)**
Scytalopus spillmanni (W Andes) Males	59.3 ± 0.6 (59.0 -60.0) (n=3)	44.0 ± 4.2 (41.0 -47.0) (n=2)	24.0 ± 1.0 (23.0 -25.0) (n=3)	15.0 ± 0.9 (14.0 -15.5) (n=3)	24.4 ± 2.1 (23.0 -26.8) (n=5)†
Scytalopus spillmanni (W Andes) Females	56.5 ± 0.7 (56.0 -57.0) (n=2)	42.5 ± 0.7 (42.0 -43.0) (n=2)	23.0 ± 0.0 (23.0 -23.0) (n=2)	14.0 ± 0.0 (14.0 -14.0 (n=2)	23.0 ± .14 (22.0 -24.0) (n=2)†
S. g. griseicollis	54.9 ± 2.5 (50.0 -61.0) (n=41)	39.8 ± 1.9 (36.5-43.5) (n=28)	22.0 ± 0.9 (20.0-23.5) (n=43)	12.7 ± 0.7 (11.0 -14.0) (n=38)	17.1 ± 2.6 (11.0 -21.0) (n=12)
S. g. griseicollis Males	55.5 ± 2.5 (52.0 -61.0) (n=22)	39.9 ± 1.6 (38.0 -43.5) (n=15)	22.2 ± 0.9 (20.0 -23.5) (n=22)	12.9 ± 0.7 (11.0 -14.0) (n=22)	17.5 ± 3.0 (11.0 -21.0) (n=8)
S. g. griseicollis Females	54.8 ± 2.5 (50.0 -59.0) (n=9)	38.7 ± 1.8 (36.5 -41.0) (n=7)	21.5 ± 0.7 (20.5 -22.5) (n=8)	12.3 ± 0.7 (11.5 -13.0) (n=8)	16.5 ± 1.9 (16.0 -18.0) (n=4)
S. griseicollis (Santander-Tamá)	55.5 ± 2.6 (52.0 -60.0) (n=11)	40.3 ± 3.1 (34.0 -44.0) (n=11)	21.4 ± 0.8 (20.5 -22.5) (n=10)	12.6 ± 0.6 (11.5 -13.5) (n=10)	16.3 ± 0.7 (15.0 -17.0) (n=6)
S. griseicollis (Santander-Tamá) Males	57.0 ± 2.0 (55.0 -60.0) (n=5)	41.2 ± 2.5 (38.5 -44.0) (n=5)	21.9 ± 0.8 (21.5-22.5) (n=5)	12.8 ± 0.5 (12.0 -13.5) (n=5)	16.8 ± 0.4 (16.3 -17.0) (n=3)
S. griseicollis (Santander-Tamá) Females	54.3 ± 2.6 (52.0 -58.0) (n=6)	39.6 ± 3.5 (34.0 -43.5) (n=6)	21.0 ± 0.5 (20.5 -22.0) (n=5)	12.4 ± 0.6 (11.5 -13.0) (n=4)	15.8 ± 0.8 (15.0 -16.0) (n=3)
S. griseicollis gilesi Males	57.0 ± 1.0 (56.0 -58.0) (n=3)	44.3 ± 0.6 (44.0 -45.0) (n=3)	22.5 ± 0.5 (22.0 -23.0) (n=3)	13.6 ± 0.4 (13.0 -14.0) (n=3)	17.8 ± 0.4 (17.5 -18.0) (n=2)
S. sp. (Perijá)	51.9 ± 2.5 (48.0 -55.0) (n=28)	38.5 ± 1.5 (36.0 -42.5) (n=26)	21.1 ± 1.0 (18.5 -22.5) (n=27)	14.0 ± 0.6 (13.0 -15.5) (n=22)	/
S. sp. (Perijá) Males	52.7 ± 2.6 (49.0 -55.0) (n=11)	39.4 ± 1.7 (37.0 -42.5) (n=10)	21.6 ± 0.9 (19.5 -22.5) (n=11)	14.3 ± 0.5 (13.5 -15.5) (n=10)	/
S. sp. (Perijá) Females	51.9 ± 2.3 (48.0 -54.0) (n=12)	38.3 ± 1.2 (37.0 -40.0) (n=11)	20.9 ± 0.9 (19.5 -22.5) (n=12)	13.8 ± 0.5 (13.0 -14.5) (n=9)	/
S. meridanus (inc. "*S. fuscicauda*")	50.8 ± 2.2 (46.0 -55.0) (n=45)	38.4 ± 2.2 (34.0 -43.0) (n=37)	21.3 ± 0.9 (20.0 -23.0) (n=45)	13.0 ± 0.6 (12.0 -14.0) (n=42)	/
S. meridanus Males	50.9 ± 2.5 (48.0 -54.0) (n=8)	40.2 ± 1.9 (38.0 -43.0) (n=6)	21.5 ± 0.8 (20.5 -23.0) (n=8)	13.4 ± 0.6 (12.5 -4.0) (n=8)	/
S. meridanus Females	50.1 ± 2.3 (44.0 -53.0) (n=22)	37.3 ± 2.0 (34.0 -43.0) (n=16)	20.9 ± 0.7 (19.5 -22.5) (n=22)	12.9 ± 0.7 (12.0 -14.0) (n=20)	/
S. canus canus	49.0 ± 2.9 (47.0 -51.0) (n=2)	34.0 ± 1.4 (33.0 -35.0) (n=2)	21.5 ± 0.7 (21.0 -22.0) (n=2)	12.5 ± 0.7 (12.0 -13.0) (n=2)	/
S. cf. canus opacus	50.5 ± 2.1 (49.0 -52.0) (n=2)	36.5 ± 0.7 (36.0 -37.0) (n=2)	20.8 ± 1.1 (20.0 -21.5) (n=2)	11.8 ± 0.4 (11.5 -12.0) (n=2)	/

† A recent capture apparently of this population (data not included above) massed 20 g (Pulgarín 2007).

APPENDIX 3: VOCAL VARIABLES OF TAXA AND POPULATIONS OF *SCYTALOPUS* DISCUSSED IN THIS PAPER. For each species and call, data is presented as follows: mean ± standard deviation (minimum - maximum) (n= number of specimens). Numbers in the second column refer to number of recordings and spectrograms inspected for the purposes of minimum and maximum data recorded values. XC refers to www.xeno-canto.org catalogue numbers. IAVH refers to IAVH's sound archive catalogue numbers.

A. Gazzetteer of recording localities:

S. g. griseicollis: Rogitama, mun. Arcabuco, Boyacá, Colombia (05°47'N, 73°31'W, 2500m) (J. Zuluaga, R. Chavarro & J. Beckers recordings); Soatá, Boyacá, Colombia (05°07'N, 73°07'W) (O. Cortés, A. Hernández & O. Laverde recordings); SFF Igüaque, Boyacá, Colombia (Sector Carrizal) (05º44'N, 73º31'W, 2800 m) (J. Zuluaga recordings); Reserva Privada el Secreto, Vereda Ciénaga-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) (O. Laverde recording); PNN Chingaza, Cundinamarca, Colombia (J. Parra & O. Laverde recordings); Monserrate, Bogotá, Cundinamarca, Colombia (J. Beckers recordings); Quebrada La Vieja, Bogotá, Colombia (2900m) (D. Knapp recording: XC 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. g. gilesi: Alto Cantagallos, mun. San Vicente de Chucurí, Serranía de los Yariguíes, Santander, Colombia (06°49'N, 73°22'W, 2450m) (TMD recordings: XC 18457, 18458, 18459 and others); Lepipuerto, mun. El Carmen / Simacota, Serranía de los Yariguíes, Santander, Colombia (6°28'N, 73°28'W, 2900m) (TMD recordings: XC 18471, 18472, 18473, 18475, 18476, 18477, 18478 and others); Filo Pamplona, Mun. Galán, Serranía de los Yariguíes, Santander, Colombia (06º38'N, 73º24'W, 3200m) (TMD & JEAC recordings XC 18452, 18453, 18454, 18455, 18456 and others).

S. griseicollis Santander-Tamá subspecies: Tamá, Río Oría, Apure state, Venezuela (2350-2410 m) (C. Parrish recordings: XC 6079, 16655, 16656, 16657, 16658, 16659, 16660, 16661); Páramo el Judio, Apure (2730 m) (C. Parrish recording: XC 16654); Suratá, Santander (07°23'N, 73°00W, 3000m) (JEAC recordings); Vereda Carrizal, Norte de Santander (S. Córdoba-C. recording: IAVH 8812).

S. meridanus: 10 km SE of La Azulita, Mérida, Venezuela, 2300m (C. Parrish & A. Spencer recordings: XC 6234, 6235, 6236, 14790); Pico Humboldt Trail, Parque Nacional Sierra Nevada, Mérida, Venezuela, 2500m (N. Athanas & A. Spencer recordings: XC 8249 and 11243); Páramo de Zumbador, Táchira, Venezuela (2500-2700m) (Boesman 1999); Yacumbu NP, Lara, Venezuela (1700m) (Boesman 1999); Laguna Mucubaji area, Mérida, Venezuela (3200m) (Boesman 1999); Páramo de Batallón, Táchira, Venezuela (2700-2900m) (Boesman 1999); Humucaro Alto, Lara, Venezuela (2650m) (Boesman 1999); Güaramacal NP, Trujillo, Venezuela (2400-2600m) (Boesman 1999).

S. spillmanni Ecuador recordings: Bellavista, Tandayapa (2200m) (W. Halfwerk recordings: XC 1480, 4217, 4218, 4219; N. Athanas recording: XC 11544); Old Chiriboga Road, Pichincha (1800m) (D. Jones recording: XC 3997); Las Palmas, Cotopaxi (00°35'S, 79°00W) (recording 44.1 in Krabbe et al. 2001); Las Palmas, Cotopaxi (2340m) (track 9.1 in Krabbe & Nilsson 2004), Hotel Bellavista, SW above Tandayapa, Pichincha (2250-2300m) (tracks 9.2, 9.3, 9.9, 9.10, 9.12, 9.14, 9.21 and 9.25 in Krabbe & Nilsson 2004; track 44.2 in Krabbe et al. 2001), San José, Tandayapa ridge, Pichincha (2300m) (tracks 9.4, 9.5, 9.16, 9.19 and 9.32 in Krabbe & Nilsson 2004), Cordillera Güacamayos, Napo (1700-2300m) (tracks 9.6, 9.13, 9.15, 9.18, 9.26, 9.28 and 9.29 in Krabbe & Nilsson 2004; track 44.4 in Krabbe et al. 2001), Orregán, Chimborazo (3145m) (tracks 9.7 and 9.8 in Krabbe & Nilsson 2004), Quebrada las Ollas, Santa Bárbara - La Bonita Road, Sucumbíos (2150m) (tracks 9.11, 9.23 and 9.31 in Krabbe & Nilsson 2004; track 44.3 in Krabbe et al. 2001), Playa, Napo (3300m) (track 9.17 in Krabbe & Nilsson 2004), Loma Bahamonte, old Santo Domingo road, Pichincha (2450-2900m) (track 9.20 in Krabbe & Nilsson 2004), NW slope Volcán Tungurahua, Tungurahua (3100m) (track 9.22 in Krabbe & Nilsson 2004), Tambo de Ashilán, upper Río Upano, Morona-Santiago (3030-3150m) (tracks 9.24 and 9.27 in Krabbe & Nilsson 2004), SW slope, Volcán Corazón, Pichincha (3150 -3850m) (track 9.30 in Krabbe & Nilsson 2004); Quebrada el Recreo, Imbrarura (00°24'N, 78° 27'W) (track 44.5 in Krabbe et al. 2001).

S. spillmanni Western Andes recordings: (not analysed in detail due to small sample size): PNN Munchique, Cauca (2600m) (O. Cortés recordings); Cuchilla La Linea-La Cumbre, Pueblo Rico, Risaralda (05°14’N 76°02’W) (IAVH 15768: Álvarez-R. et al. 2007).

S. spillmanni Central Andes recordings: Ibagué, El Rancho, road to Nevado del Tolima, Tolima (L.E. Urueña recordings); Reserva Natural Ibanasca, Ibagué, Tolima (04°36’N; 75°15W, 2300-2600 m) (O. Laverde recordings: IAVH 24179, 24188, 24237, 24242, 24245, 24251, 24284, 24287); Reserva Natural Río Blanco, Manizales, Caldas (05°05’N 75° 21’W, 2550-3600m) (O. Laverde recordings: IAVH 24504, 24516, 24624, 24632, 24672; D. Bradley recordings: XC 17623, 17624; IAVH 30903: Álvarez et al. 2007; Álvarez-R. & Córdoba-C. 2002); Parque Regional Ucumarí, Pereira, Risaralda (04° 43’N 75°35’W) (IAVH 6807: Álvarez-R. et al. 2007); Finca los Molinos, corregimiento de Dantas, Ibagué, Tolima (04°34’N 75°16’W; 2000-2200 m) (O. Laverde recording: IAVH 17271); Vereda El Laurel, Hacienda Termópilas, Aranzazu, Caldas (5° 14 N, 75°29’ W, 2250m) (S. Córdoba-C recording: IAVH 7900); Reserva Los Yalcones, San Agustín, Huila (01° 49 N, 76°21’W, 2322-2430m) (D. Calderón recording: IAVH 16625); RNA El Mirador, Génova, Quindío (2900 m) (F. Lambert recording: XC 17623).

S. spillmanni Eastern Andes recordings: La Aurora, finca Pamplona, Serranía de los Yariguíes, vereda San Isidro, municipio Galán, Santander Dept, Colombia (06º 38’ N; 73º 24’ W; 2700 m) (TMD & JEAC recordings: XC 18486, 18687, 18488 and others), Lepipuerto, mun. El Carmen / Simacota, Serranía de los Yariguíes, Santander, Colombia (6°28’N, 73° 28’W, 2900m) (TMD recordings: XC 18489, 18490 and others); Finca La Carbonera, Los Robles, La Agüadita, Fusagasugá, Cundinamarca (4°25’N, 74° 19’W, 2450-2550m) (O. Laverde recordings: IAVH 17854, 17855, 17856, 17857, 17884, 17917, 17939, 17940); Vereda Carrizal, Norte de Santander (S. Córdoba-C. recording: IAVH 8645).

“*S. cf. canus opacus* undescribed southern race”: see Krabbe et al. (2001) and Krabbe & Nilsson (2004) for localities.

S. latrans, S. atratus and *S. rodriguezi sp.*: Various Serranía de los Yariguíes recordings by the authors and published recordings in Álvarez et al. 2007 and Krabbe & Nilsson (2004).

B. Measurements of vocal variables of taxa and populations of *Scytalopus* discussed in this paper.

Call type / *Taxon and region*	No. of calls / no. of recordings	Duration (s)	No. of notes	Pace (Notes/s)	Max. frequency of lowest note (kHz)	Max. frequency of highest note (kHz)	Frequency variation (kHz)	Note shape
Reeling songs (data for flat and rising songs combined)								
Scytalopus spillmanni (Ecuador)	171/32: Rising: 123/21: Chiriboga (3/1), Mindo (1/1), Tandayapa (36/9) Güacamayos (57/5), Las Palmas (1/1), Orregán (1/1), Las Ollas (3/1), Volcán Corazón (20/1), Las Palmas (1/1). Flat: 48/11: Chiraboga (3/1), Güacamayos (3/2), Tandayapa (34/6), Playa (5/1), Las Ollas (3/1).	4.12 ± 9.03 (0.08-68.75) (n=57)	130.35 ± 263.66 (3.00-1856.00) (n=66)	34.02 ± 3.36 (27.00-42.86) (n=57)	3.11 ± 0.39 (2.40-4.20) (n=66)	3.68 ± 0.47 (2.70-4.90) (n=66)	0.57 ± 0.32 (0.10-1.60) (n=66)	Rising: Up-down strokes with some double-notes (56%); downstrokes, some with faint leading upstroke (44%). Flat: Downstrokes, some with faint leading upstroke (78%), updownstrokes (including broad blobs with up and down tails and soe double notes) (22%).
Scytalopus spillmanni (C Andes)	68/19: Rising: 20/7: Ibagué road to Nevado (1/1), Ibanasca (3/1), Ucumarí (1/1), Río Blanco (12/2), San Agustín (2/1) and Génova (1/1). Flat: 48/12: Los Molinos (1/1), Ibanasca (5/3), Rio Blanco (17/5), Ucumarí (1/1), Ibagué road to Nevado (2/1) and Aranzazu (22/1)	5.86 ± 4.88 (0.35-14.10) (n=31)	155.01 ± 130.15 (10.00-504.00) (n=34)	28.72 ± 3.01 (22.00-36.21) (n=33)	2.76 ± 0.25 (2.35-3.25) (n=34)	3.01 ± 0.31 (2.55-3.90) (n=34)	0.26 ± 0.16 (0.10-0.70) (n=34)	Rising: Up-down strokes with some double-notes (100%). Flat: Upstrokes, some with faint leading upstroke (20%), up-down strokes with some double notes (80%)
Scytalopus spillmanni subsp. (Eastern Andes)	43/17: Rising: 37/14: Yariguíes (17/8: all La Aurora) and Fusagasugá (20/6). Flat: 6/3: Yariguíes (1/1: La Aurora), Fusagasugá (1/1) and Carrizal (4/1).	5.54 ± 4.83 (0.62-13.50) (n=18)	169.00 ± 141.23 (20.00-369.00) (n=26)	29.07 ± 2.12 (25.33-32.98) (n=17)	3.13 ± 0.26 (2.80-3.60) (n=26)	3.68 ± 0.25 (3.20-4.10) (n=25)	0.53 ± 0.19 (0.20-0.90) (n=25)	Up-down strokes with some double-notes (100%).
Scytalopus griseicollis griseicollis (Eastern Andes)	111/24: Rising: 66/7: Bogotá (1/1), Chingaza (42/3), Iguaque (5/1) & Soatá (18/2). Flat: 45/15: Chingaza (23/9), Iguaque (4/1), Soatá (3/1), Fusagasugá (6/1) Monserrate (2/1), La Vieja (4/1) and Rogitama (3/1).	2.22 ± 3.19 (0.15-13.35) (n=57)	53.39 ± 73.77 (4.00-294.00) (n=56)	24.98 ± 3.20 (20.00-32.00) (n=57)	2.37 ± 0.24 (1.70-2.90) (n=55)	2.80 ± 0.20 (2.50-3.40) (n=57)	0.42 ± 0.21 (0.10-1.20) (n=54)	Up-down strokes (100%)

Call type / *Taxon and region*	No. of calls / no. of recordings	Duration (s)	No. of notes	Pace (Notes/s)	Max. frequency of lowest note (kHz)	Max. frequency of highest note (kHz)	Frequency variation (kHz)	Note shape
Scytalopus griseicollis subsp. (Santander-Tamá)	60/9: Rising: 49/6 Tamá Venezuela (23/4) Suratá (26/2). Flat: 11/3: Tamá Venezuela (8/2) and Suratá (3/1).	1.25 ± 0.59 (0.46-3.10) (n=25)	32.49 ± 11.80 (16.00-71.00) (n=25)	27.19 ± 4.13 (22.00-35.42) (n=27)	2.33 ± 0.39 (1.80-2.90) (n=26)	2.88 ± 0.20 (2.45-3.15) (n=27)	0.57 ± 0.30 (0.10-1.10) (n=26)	Up-down strokes (100%)
Scytalopus griseicollis gilesi	39/11: Rising: 33/8: Lepipuerto (32/7) and Filo Pamplona (1/1). Flat: 6/3: Lepipuerto (3/1) and Filo Pamplona (3/2).	1.12 ± 0.34 (0.65-2.00) (n=21)	26.11 ± 10.31 (18.00-60.00) (n=19)	23.31 ± 3.67 (19.00-30.00) (n=23)	2.33 ± 0.36 (2.30-3.00) (n=16)	2.61 ± 0.23 (2.00-3.30) (n=26)	0.37 ± 0.16 (0.10-0.60) (n=14)	Up-down strokes (100%)
S. meridanus	Flat: 10/7: La Aazulita (1/1), Pico Humboldt (2/2), Páramo de Zumbador (1/1) Yacumbu NP (4/1), Guaramacal NP (1/1), Mucubaji (1/1) and Humucaro Alto (1/1).	15.46 ± 8.00 (7.80-31.90) (n=9)	214.86 ± 117.72 (68.00-479.00) (n=9)	14.10 ± 3.60 (8.50-19.80) (n=9)	3.38 ± 0.24 (3.00-3.90) (n=9)	3.96 ± 0.23 (3.60-4.40) (n=9)	0.48 ± 0.16 (0.30-0.80) (n=9)	Fast downstrokes or lines (100%).
S. meridanus Slower Song	7/5: La Azulita (2/2) Páramo de Zumbador (1/1) and Güaramacal NP (1/1).	23.30 ± 20.25 (5.20 -61.20) (n=7)	180.86 ± 147.54 (42.00-441.00) (n=7)	7.98 ± 1.74 (6.19-11.50) (n=7)	3.41 ± 0.46 (2.70-4.20) (n=7)	4.64 ± 0.26 (4.20-4.90) (n=7)	1.23 ± 0.49 (0.50-1.90) (n=7)	Fast downstrokes or lines (100%).
"Scytalopus canus opacus undescribed southern race" (S. Ecuador & Peru)	Flat: 21/5: see Krabbe et al. (2001) and Krabbe & Nilsson (2004).	7.14 ± 4.72 (0.20-22.25) (n=11)	229.27 ± 160.26 (6.00-534.00) (n=12)	31.99 ± 5.64 (21.33-41.00) (n=11)	4.11 ± 0.31 (3.55-4.60) (n=12)	4.43 ± 0.28 (4.00-4.85) (n=12)	0.31 ± 0.18 (0.10-0.65) (n=12)	Downstrokes, sometimes with thin upstroke (60%); lines (40%).
Scolds								
Scytalopus spillmanni (Ecuador)	94/10: Güacamayos (9/1), Tandayapa (10/1), Bahamonte (2/1), Volcán Tunurahua (10/1), Playa (3/1), Las Ollas (21/2), San José (13/2) and Tambo de Ashilán (26/1).	0.94 ± 0.27 (0.24-1.49) (n=29)	15.41 ± 4.86 (5.00 -22.00) (n=29)	16.53 ± 3.71 (10.87-23.26) (n=29)	3.73 ± 0.38 (3.10-4.90) (n=29)	4.27 ± 0.36 (3.75-5.15) (n=29)	0.54 ± 0.28 (0.05-1.30) (n=29)	Up-down stroke (90%), blob with faint upstroke (10%).
Scytalopus spillmanni (C Andes)	41/5: Ibagué road to Nevado (3/1), Ibanasca (32/3) and Río Blanco (6/1).	1.04 ± 0.17 (0.77-1.32) (n=15)	16.13 ± 1.92 (13.00-20.00) (n=15)	15.81 ± 2.06 (12.57-18.18) (n=15)	3.17 ± 0.28 (2.55-3.50) (n=15)	3.60 ± 0.18 (3.25-3.90) (n=15)	0.43 ± 0.16 (0.20-0.75) (n=15)	Up-down stroke (100%).

Call type / *Taxon and region*	**No. of calls / no. of recordings**	**Duration (s)**	**No. of notes**	**Pace (Notes/s)**	**Max. frequency of lowest note (kHz)**	**Max. frequency of highest note (kHz)**	**Frequency variation (kHz)**	**Note shape**
Scytalopus spillmanni subsp. (Eastern Andes)	60/8: Yariguíes (26/6, of which Lepipuerto 5/2 and La Aurora 21/4) and Fusagasugá (34/2).	1.07 ± 0.11 (0.85-1.23) (n=15)	19.00 ± 1.81 (14.00-22.00) (n=19)	17.74 ± 1.90 (13.93-21.78) (n=15)	3.83 ± 0.20 (3.30 -4.25) (n=16)	4.17 ± 0.25 (3.70 -4.60) (n=17)	0.37 ± 0.11 (0.10-1.00) (n=16)	Up-down stroke (60%); blob with faint downstroke (40%).
Scytalopus griseicollis griseicollis (Eastern Andes)	152/20: Rogitama (38/5), Chingaza (92/11); Soatá (4/2), Garagoa (7/1), Bojacá (8/1), Fusagasugá (2/1) and Monserrate (1/1).	1.19 ± 0.30 (0.55-2.00) (n=53)	32.36 ± 8.35 (16.00-52.00) (n=42)	28.21 ± 1.89 (24.83-32.31) (n=42)	2.91 ± 0.28 (2.20 -3.70) (n=53)	3.72 ± 0.26 (3.00 -4.20) (n=53)	0.81 ± 0.26 (0.20-1.50) (n=53)	Up-down stroke with stronger upstroke (100%).
Scytalopus griseicollis subsp. (Santander-Tamá)	49/6: Tamá Colombia (3/1) and Tamá Venezuela (46/5).	0.99 ± 0.11 (0.80-1.30) (n=15)	28.80 ± 5.56 (23.00-46.00) (n=15)	29.05 ± 2.42 (26.36-35.38) (n=15)	2.90 ± 0.23 (2.40 -3.30) (n=14)	3.97 ± 0.14 (3.70 -4.50) (n=18)	1.03 ± 0.27 (0.60-1.75) (n=14)	Up-down stroke with stronger upstroke (100%).
Scytalopus griseicollis gilesi	75/13: Alto Cantagallos (19/3), Lepipuerto (30/7) and Filo Pamplona (26/4).	1.11 ± 0.17 (0.70-1.50) (n=33)	31.36 ± 4.94 (21.00-43.00) (n=32)	28.10 ± 2.64 (21.82-33.64) (n=32)	2.39 ± 0.31 (1.70 -2.90) (n=33)	3.20 ± 0.26 (2.60 -3.60) (n=33)	0.81 ± 0.31 (0.30-1.70) (n=33)	Up-down stroke with stronger upstroke (100%).
S. meridanus	14/3: Páramo de Batallón (7/1), Güaramacal NP (6/1) and La Azulita (1/1).	1.16 ± 0.30 (0.75-1.60) (n=7)	21.14 ± 6.47 (12.00-31.00) (n=7)	18.06 ± 1.04 (16.00-19.23) (n=7)	4.96 ± 0.23 (4.70 -5.30) (n=7)	5.44 ± 0.20 (5.20 -5.70) (n=7)	(0.20-0.80) (n=7)	Downstrokes (100%).
"*S. cf. canus opacus* undescribed southern race" (S. Ecuador & Peru)	64/8: see Krabbe et al. (2001) and Krabbe & Nilsson (2004).	0.94 ± 0.14 (0.65-1.26) (n=21)	23.89 ± 4.27 (17.00-33.00) (n=21)	25.47 ± 2.54 (20.59-30.00) (n=21)	3.97 ± 0.27 (3.20 -4.40) (n=21)	4.44 ± 0.19 (3.95 -4.85) (n=21)	0.48 ± 0.21 (0.05-1.05) (n=21)	Up-down stroke with stronger downstroke (100%)

APPENDIX 4: DIFFERENCES BETWEEN *S. SPILLMANNI*, *S. GRISEICOLLIS* AND *S. MERIDANUS* Shading shows proposed species limits resulting from this article, defined by populations diagnosable to at least Level 5 by voice (for *S. spillmanni*, using data from the Eastern Andes population only). Differences marked with a question mark or without Level 1 did not pass test of statistical significance. Degrees of freedom for vocal data are presented for (song speed/acoustic frequency. Degrees of freedom for biometric data are presented for (wing/tail/tarsus/culmen/mass).

	***S. spillmanni* Western Ecuador**	***S. spillmanni* Eastern Ecuador**	***S. spillmanni* Central Andes**	***S. spillmanni* Eastern Andes**	***S. g. griseicollis***	***S. g. gilesi***	***S. griseicollis* (Santander-Tamá subsp.)**	***S. meridanus / S. fuscicauda***
***S. spillmanni* Western Ecuador**								
Reeling song (d.f.=23/35)	X	Higher (1)	Faster (1) Higher (1,2)	Faster (1) Higher (1)	Faster (1,2) Higher (1,2)	Faster (1,2,3,5) Higher (1,2,3)	Faster (1) Higher (1,2)	Faster (1,2,3,4,5) Note Shape (4)
Scold (d.f.=20/20)	X	N/A	Higher (1,2)	N/A	Slower (1,2,3,4,5) Higher (1)	Slower (1,2,3) Higher (1,2,3,4,5)	Slower (1,2,3,4,5) Higher (1)	Lower (1,2,3,4,5) Note Shape (4)
Plumage (d.f.=15)	X	N/A	N/A?	N/A	Darker (4)	Darker (4)	Darker (4)	Darker (4)
Biometrics (d.f.=22/19/8 /0/23)	X	Longer Tail?	N/A?	Longer Tarsus (1,2) Greater Mass?	Longer Wing (1,2) Longer Tail (1,2) Longer Tarsus (1,2) Greater Mass (1,2,3,4)	Longer Wing (1,2) Longer Tarsus (1,2,4) Greater Mass (1,2,3,4)	Longer Wing (1,2) Longer Tail (1) Longer Tarsus (1,2,4) Greater Mass (1,2,3,4,5)	Longer Wing (1,2,3,4,5) Longer Tail (1,2) Longer Tarsus (1,2,3,4) Greater Mass?
***S. spillmanni* Eastern Ecuador**								
Reeling song (d.f.=21/28)	Lower (1)	X	Faster (1) Higher (1,2)	Faster (1) Lower (1)	Faster (1,2) Higher (1,2)	Faster (1,2,3,5) Higher (1,2)	Faster (1) Higher (1)	Faster (1,2,3,4,5) Lower (1) Note Shape (4)
Scold (d.f.=3/7)	N/A	X	Higher?	N/A	Slower (1,2,4)	Slower (1,2,4) Higher (1,2,4)	Slower (1,2,4)	Slower (1) Lower (1,2,4) Note Shape (4)
Plumage (d.f.=2)	N/A	X	N/A?	N/A	Darker (4)	Darker (4)	Darker (4)	Darker (4)
Biometrics (d.f.=12/12/8 /0/12)	Shorter Tail?	X	N/A?	Longer Tarsus? Greater Mass?	Longer Wing (1,2) Longer Tail (1) Longer Tarsus? Greater Mass (1,2)	Longer Wing (1,2) Longer Tarsus (1) Greater Mass (1,2,4)	Longer Wing (1) Longer Tarsus (1) Greater Mass (1,2,3,4,5)	Longer Wing (1,2,3,4,5) Longer Tail (1) Longer Tarsus (1,2) Greater Mass?
***S. spillmanni* Central Andes**								
Reeling song (d.f.=31/33)	Slower (1) Lower (1,2)	Slower (1) Lower (1,2)	X	Lower (1,2)	Faster (1) Higher (1)	Faster (1,2) Higher (1)		Faster (1,2,3,4,5) Lower (1,2,3) Note Shape (4)
Scold (d.f.14/14)	Lower (1,2)	Lower?	X	Lower (1,2)	Slower (1,2,3,4,5)	Slower (1,2,3,4,5) Higher (1)	Slower (1,2,3,4,5), Lower (1,2)	Slower (1) Lower (1,2,3,4,5) Note Shape (4)
Plumage (d.f.=1)	N/A?	N/A?	X	Lighter?	Darker (4)	Darker (4)	Darker (4)	Darker (4)

	***S. spillmanni* Western Ecuador**	***S. spillmanni* Eastern Ecuador**	***S. spillmanni* Central Andes**	***S. spillmanni* Eastern Andes**	***S. g. griseicollis***	***S. g. gilesi***	***S. griseicollis* (Santander-Tamá subsp.)**	***S. meridanus / S. fuscicauda***
Biometrics (d.f.=1/1/1/1/0)	N/A?	N/A?	X	Longer Tarsus (4) Greater Mass (4)	Longer Tarsus (4) Greater Mass (4)	Shorter Tail (4), Longer Tarsus (4) Greater Mass (4)	Longer Tarsus (4) Greater Mass (4)	Longer Wing (1,4) Longer Tarsus (4) Greater Mass?
***S. spillmanni* Eastern Andes**								
Reeling song (d.f.=16/25)	Slower (1) Lower (1)	Slower (1) Higher (1)	Higher (1,2)	X	Faster (1) Higher (1,2,3)	Faster (1,2) Higher (1,2,3,5)	Higher (1,2,4)	Faster (1,2,3,4,5) Lower (1) Note Shape (4)
Scold (d.f.=17/19)	N/A	N/A	Higher (1,2)	X	Slower (1,2,3,4,5) Higher (1)	Slower (1,2,3,4,5) Higher (1,2,3,4)	Slower (1,2,3,4,5) Higher?,	Lower (1,2,3,4,5) Note Shape (4)
Plumage (d.f.=4)	N/A	N/A	Darker?	X	Darker (4)	Darker (4)		Darker (4)
Biometrics (d.f.=2/2/2/2/0)	Shorter Tarsus (1,2) Lower Mass?	Shorter Tarsus? Lower Mass?	Shorter Tarsus (4) Lower Mass (4)	X	Longer Tarsus? Greater Mass (4)	Greater Mass (4)	Longer Tarsus (4) Greater Mass (4)	Longer Wing (4) Longer Tarsus? Greater Mass?
S. g. griseicollis								
Reeling song (d.f.=56/56)	Slower (1,2) Lower (1,2)	Slower (1,2) Lower (1,2)	Slower (1) Lower (1)	Slower (1) Lower (1,2,3)	X	Faster (1) Higher (1)		Faster (1,2,4) Lower (1,2,3,4,5) Note Shape (4)
Scold (d.f.=41/52)	Faster (1,2,3,4,5) Lower (1)	Faster (1,2,4)	Faster (1,2,3,4,5)	Faster (1,2,3,4,5) Lower (1)	X	Higher (1)	Lower (1)	Faster (1,2,3,4,5) Lower (1,2,3,4,5) Note Shape (4)
Plumage (d.f.=56)	Lighter (4)	Lighter (4)	Lighter (4)	Lighter (4)	X	Lighter (4)	Grayer Back (4)	Direct comparison not possible
Biometrics (d.f.=21/14/21/21/7)	Shorter Wing (1,2) Shorter Tail (1,2) Shorter Tarsus (1,2) Lower Mass (1,2,3,4)	Shorter Wing (1,2) Shorter Tail (1) Shorter Tarsus? Lower Mass (1,2)	Shorter Tarsus (4), Lower Mass (4)	Shorter Tarsus? Lower Mass (4)	X	Shorter Tail (1,2,4)		Longer Wing (1) Longer Tarsus? Longer Bill?
S. g. gilesi								
Reeling song (d.f.=41/44)	Slower (1,2,3,5) Lower (1,2,3)	Slower (1,2,3,5) Lower (1,2)	Slower (1,2) Lower (1)	Slower (1,2) Lower (1,2,3,5)	Slower (1) Lower (1)	X	Slower (1) Lower (1)	Faster (1,2) Lower (1,2,3,4,5) Note Shape (4)
Scold (d.f.=31/32)	Faster (1,2,3) Lower (1,2,3,4,5)	Faster (1,2,4) Lower (1,2,4)	Faster (1,2,3,4,5) Lower (1)	Faster (1,2,3,4,5) Lower (1,2,3,4)	Lower (1)	X	Lower (1,2,4)	Faster (1,2,3,4,5) Lower (1,2,3,4,5) Note Shape (4)
Plumage (d.f.=2)	Lighter (4)	Lighter (4)	Lighter (4)	Lighter (4)	Darker (4)	X	Grayer Back (4)	Direct comparison not possible
Biometrics (d.f.=2/2/2/2/1)	Shorter Wing (1,2) Shorter Tarsus (1,2,4) Lower Mass (1,2,3,4)	Shorter Wing (1,2) Shorter Tarsus (1) Lower Mass (1,2,4)	Longer Tail (4) Shorter Tarsus (4) Lower Mass (4)	Lower Mass (4)	Longer Tail (1,2,4)	X	Longer Tail (4)	Longer Wing (1,2,4) Longer Tail (1,2,4) Longer Tarsus?
***S. griseicollis* Santander-Tamá subsp.**								
Reeling song (d.f.=26/26)	Slower (1) Lower (1,2) ,	Slower(1) Lower (1)		Lower (1,2,4)		Faster (1) Higher (1)	X	Faster (1,2,4) Lower (1,2,3,4,5) Note Shape (4)

	S. spillmanni **Western Ecuador**	*S. spillmanni* **Eastern Ecuador**	*S. spillmanni* **Central Andes**	*S. spillmanni* **Eastern Andes**	*S. g. griseicollis*	*S. g. gilesi*	*S. griseicollis* **(Santander-Tamá subsp.)**	*S. meridanus / S. fuscicauda*
Scold (d.f.=14/17)	Faster (1,2,3,4,5) Lower (1)	Faster (1,2,4)	Faster (1,2,3,4,5) Higher (1,2)	Faster (1,2,3,4,5) Lower?	Higher (1)	Higher (1,2,4)	X	Faster (1,2,3,4,5) Lower (1,2,3,4,5) Note Shape (4)
Plumage (d.f.=10)	Lighter (4)	Lighter (4)	Lighter (4)		Browner Back (4)	Browner Back (4)	X	Browner Back (4)
Biometrics (d.f.=4/4/4/4/2)	Shorter Wing (1,2) Shorter Tail (1) Shorter Tarsus (1,2,4) Lower Mass (1,2,3,4,5)	Shorter Wing (1) Shorter Tarsus (1) Lower Mass (1,2,3,4,5)	Shorter Tarsus (4) Lower Mass (4)	Shorter Tarsus (4) Lower Mass (4)		Shorter Tail (4)	X	Longer Wing (1,2) Longer Tarsus? Longer Bill?
S. meridanus / S. fuscicauda								
Reeling song (d.f.=8/8)	Slower (1,2,3,4,5) Note Shape (4)	Slower (1,2,3,4,5) Higher (1) Note Shape (4)	Slower (1,2,3,4,5) Higher (1,2,3) Note Shape (4)	Slower (1,2,3,4,5) Higher (1) Note Shape (4)	Slower (1,2,4) Higher (1,2,3,4,5) Note Shape (4)	Slower (1,2) Higher (1,2,3,4,5) Note Shape (4)	Slower (1,2,4) Higher (1,2,3,4,5) Note Shape (4)	X
Scold (d.f.=6/6)	Higher (1,2,3,4,5) Note Shape (4)	Faster (1) Higher (1,2,4) Note Shape (4)	Faster (1) Higher (1,2,3,4,5) Note Shape (4)	Higher (1,2,3,4,5) Note Shape (4)	Slower (1,2,3,4,5) Higher (1,2,3,4,5) Note Shape (4)	Slower (1,2,3,4,5) Higher (1,2,3,4,5) Note Shape (4)	Slower (1,2,3,4,5) Higher (1,2,3,4,5) Note Shape (4)	X
Plumage (d.f.=58)	Lighter (4)	Lighter (4)	Lighter (4)	Lighter (4)	Direct comparison not possible	Direct comparison not possible	Grayer Back (4)	X
Biometrics (d.f.=6/4/5/6/0)	Shorter Wing (1,2,3,4,5) Shorter Tail (1,2) Shorter Tarsus (1,2,3,4) Lower Mass?	Shorter Wing (1,2,3,4,5) Shorter Tail (1) Shorter Tarsus (1,2) Lower Mass?	Shorter Wing (1,4) Shorter Tarsus (4) Lower Mass?	Shorter Wing (4) Shorter Tarsus? Lower Mass?	Shorter Wing (1) Shorter Tarsus? Shorter Bill?	Shorter Wing (1,2,4) Shorter Tail (1,2,4) Shorter Tarsus?	Shorter Wing (1,2) Shorter Tarsus? Shorter Bill?	X