A new species of tapaculo (Rhinocryptidae: Scytalopus) from the Serranía de Perijá of Colombia and Venezuela

Authors: Avendaño, Jorge Enrique, Cuervo, Andrés M., López-O., Juan Pablo, Gutiérrez-Pinto, Natalia, Cortés-Diago, Alexander, et al.

Source: The Auk, 132(2) : 450-466

Published By: American Ornithological Society

URL: https://doi.org/10.1642/AUK-14-166.1

The Auk
Ornithological Advances

www.aou.org

Volume 132, 2015, pp. 450–466
DOI: 10.1642/AUK-14-166.1

RESEARCH ARTICLE

A new species of tapaculo (Rhinocryptidae: *Scytalopus*) from the Serranía de Perijá of Colombia and Venezuela

Jorge Enrique Avendaño,[1a]* Andrés M. Cuervo,[2,3] Juan Pablo López-O.,[4] Natalia Gutiérrez-Pinto,[1,5] Alexander Cortés-Diago,[6] and Carlos Daniel Cadena[1]

[1] Laboratorio de Biología Evolutiva de Vertebrados, Departamento de Ciencias Biológicas, Universidad de los Andes, Bogotá, Colombia
[2] Department of Biological Sciences and Museum of Natural Science, Louisiana State University, Baton Rouge, Louisiana, USA
[3] Department of Ecology and Evolutionary Biology, Tulane University, New Orleans, Louisiana, USA
[4] Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia
[5] Department of Biology, University of Miami, Coral Gables, Florida, USA
[6] Fundacion EcoHabitats, Popayán, Colombia
[a] Current address: Programa de Biología y Museo de Historia Natural, Universidad de los Llanos, Sede Barcelona, Villavicencio, Colombia
* Corresponding author: jorgeavec@gmail.com

Submitted July 14, 2014; Accepted December 22, 2014; Published March 11, 2015

ABSTRACT

We describe *Scytalopus perijanus* (Perijá Tapaculo), a new species in the family Rhinocryptidae (suborder Tyranni) found in humid montane and elfin forests (1,600–3,225 m elevation) in the Serranía de Perijá of Colombia and Venezuela. Although specimens of this taxon have been available in museums since 1941, they were not carefully studied and were ascribed to different taxa of the *latebricola* and *atratus* groups. We obtained a modern series of specimens that, coupled with analysis of vocal and genetic data, clarified this taxonomic puzzle. The new *Scytalopus* exhibits distinctive morphological and vocal traits with respect to all other known species and represents a differentiated evolutionary lineage within a clade of northern species, including *S. meridanus*, *S. caracae*, and *S. latebricola*. The new species has not been recorded in sympatry with any other *Scytalopus*, but it may overlap at lower elevations with *S. atratus nigricans*, although each uses different microhabitats. Ecological niche modeling indicates that the new species currently has a restricted geographic range within the Serranía de Perijá, where large extents of natural habitat have been cleared and fragmented, particularly on the Colombian slopes. *Scytalopus perijanus*, however, is uncommon to fairly common in forest fragments, tall secondary forest patches, elfin forest, and paramo vegetation at the treeline.

Keywords: Andes, cloud forest, nest, paramo, systematics, tracheophone suboscines, Scytalopodinae, vocalizations

Una nueva especie de tapaculo (Rhinocryptidae: *Scytalopus*) de la Serranía de Perijá de Colombia y Venezuela

RESUMEN

Describimos a *Scytalopus perijanus* (Tapaculo de Perijá), una nueva especie de la familia Rhinocryptidae (suborden Tyranni) del bosque montano alto y páramo (1,600 a 3,225 m) de la Serranía de Perijá de Colombia y Venezuela. Aunque han existido especímenes de este taxón en museos desde 1941, éstos no habían sido estudiados con cuidado y fueron asignados a diferentes taxones de los grupos *latebricola* y *atratus*. Recolectamos una serie moderna de especímenes que, junto con análisis de datos vocales y genéticos, aclararon este acertijo taxonómico. El nuevo *Scytalopus* exhibe rasgos distintivos morfologicos y vocales con respecto a todas las otras especies conocidas y representa un linaje evolutivo distinto en un clado de especies del norte, incluyendo a *S. meridanus*, *S. caracae* y *S. latebricola*. La nueva especie no ha sido registrada en simpatría con ningún otro *Scytalopus*, pero podría solaparse a menores elevaciones con *S. atratus nigricans*, aunque cada una usa microhábitats diferentes. Los modelos de nicho ecológico indican que la distribución potencial de la nueva especie actualmente está restringida en la Serranía de Perijá, donde se han perdido o fragmentado amplias áreas de hábitat natural principalmente en las laderas colombianas. Sin embargo, *S. perijanus* es poco a moderadamente común en fragmentos de bosque, en los parches de bosque secundario alto, en el bosque enano y en la vegetación de páramo colindante con el bosque.

Palabras clave: Andes, bosque nublado, nido, páramo, Scytalopodinae, sistemática, suboscines traqueófonos, vocalizaciones

INTRODUCTION

The genus *Scytalopus* (Rhinocryptidae) includes small, tracheophone subsocines that inhabit primarily the dense and humid understory of Neotropical montane forests. At least 28 species-level *Scytalopus* taxa have been described or reclassified in the last 20 years (excluding Brazil; Fjeldså and Krabbe 1990, Krabbe and Schulenberg 2003, Remsen et al. 2014), suggesting that even montane regions that have been explored to some extent may still harbor undescribed species in this genus. The Serranía de Perijá is a mountain spur on the Colombian–Venezuelan border projecting northward from the Eastern Andes (Cordillera Oriental) of Colombia. This range is an important area of endemism for birds and other Neotropical montane organisms (Vuilleumier 1970, Cracraft 1985, Hernández-Camacho et al. 1992), but the composition and evolutionary history of the Perijá montane avifauna have not been sufficiently studied, particularly on the Colombian (western) slope (Phelps 1943, Cuervo et al. 2014, López-O. et al. 2014). Two *Scytalopus* taxa occur in this range (Ginés et al. 1953, López-O. et al. 2014): *S. atratus nigricans* on the eastern foothills (Phelps and Phelps 1953) and an unnamed population (see Lentino et al. 2004) at higher elevations, which we formally describe herein.

In 1941 and 1942, Melbourne A. Carriker, Jr., explored the western slope of the Serranía de Perijá, collecting 27 specimens of a single species of *Scytalopus* from 6 localities, all sent to the Smithsonian Institution National Museum of Natural History (USNM; C. Ludwig personal communication). Carriker's series was mistakenly assumed to correspond to *S.* [*femoralis*] *atratus nigricans* (Carriker 1954, Meyer de Schauensee 1959), a taxon described from 2 specimens collected at lower elevations on the Venezuelan side of the range (Phelps and Phelps 1953). Carriker's specimens lack the diagnostic traits of *S. atratus nigricans*, including size, color patterns, and a white patch on the middle crown (Phelps and Phelps 1953, Hilty 2003). From 1951 to 1978, a larger series of the same taxon collected by Carriker was obtained on the eastern slope by personnel of the Adolfo Pons (PONS) and Phelps (COP) collections in Venezuela (Ginés and Yépez 1953, Aveledo Hostos and Pérez Chinchilla 1989).

The combined series of this upper montane *Scytalopus* remained unstudied for decades despite its existence in different museums since 1941. As a result, this tapaculo has not only been ascribed inconsistently to different taxa over the years, but it has also been overlooked in the literature on avian distributions and monographs on tapaculos (e.g., Phelps and Phelps 1950, Peters 1951, Meyer de Schauensee 1964, Fjeldså and Krabbe 1990, Krabbe and Schulenberg 2003, Clements et al. 2014). It was only in 1953 that this population was explicitly referred to as a member of the *latebricola* group (sensu Zimmer 1939); based on specimens at the PONS collection, it was then identified as *S. caracae* (Ginés et al. 1953, Ginés and Yépez 1953); however, most later authors referring to this population have treated it either as *meridanus* (Phelps and Phelps 1963, Viloria and Calchi La C 1993, Hilty 2003) or simply as *S. latebricola* (Ridgely and Tudor 1994). More recently, it has been hypothesized that the Perijá population could represent either an undescribed species based on vocal differences with respect to better-known Venezuelan taxa (Lentino et al. 2004; C. Sharpe and D. Ascanio personal communication) or a subspecies related to *S. griseicollis* or *S. meridanus* based on morphology (Donegan and Avendaño 2008).

In September 2006, J. P. López-O. and A. Cortés-Diago collected 2 *Scytalopus* in cloud forest at 2,450 m on the western (Colombian) slope of the Serranía de Perijá. No taxonomic identification was made from the specimens at the time due to the lack of sufficent comparative material, tape recordings, or genetic data. Between July 2008 and February 2009, however, López-O. et al. (2014) collected a modern series of 16 specimens and sound recordings of this *Scytalopus* in cloud forest, elfin forest, and paramo (2,450 and 3,050 m) in the same general region and near the area first visited by Carriker. Based on this new material, we conducted molecular phylogenetic analyses, which confirmed that the Perijá *Scytalopus* represents a unique evolutionary lineage highly divergent from all other *Scytalopus* species. Vocal, morphological, and ecological analyses further confirmed that this population represents a distinct, undescribed species, which we propose to name:

Scytalopus perijanus, sp. nov.
Perijá Tapaculo
Tapaculo de Perijá

Holotype

The holotype is an adult male specimen deposited in the ornithological collection of the Instituto de Ciencias Naturales at Universidad Nacional de Colombia (ICN), number 36745; collected from above vereda El Cinco, Municipality of Manaure, Department of Cesar, on the western slope of the Serranía de Perijá, Colombia (10°21′50″N, 72°56′51″W; ~2,450 m elevation). It was lured by a playback of a recording of its own primary song and collected on July 10, 2008, by J. E. Avendaño (field number 695). The holotype was found in a tangled edge of humid montane forest intermixed with *Chusquea* bamboo. Tissue samples of the holotype are preserved in the genetic resources collections of the Museo de Historia Natural de la Universidad de los Andes (ANDES-BT 760) and Instituto Alexander von Humboldt (IAvH-BT 11317), Colombia. Sound recordings of the holotype's vocalizations are deposited in the Colección de Sonidos Animales, Instituto Alexander von Humboldt (IAvH-CSA 2801-16).

TABLE 1. Body mass (g) and morphometric measurements (mm) of males of *S. perijanus* and selected *Scytalopus* species. Values are presented as mean and range (in parenthesis). Measurements of *S. perijanus* are from Colombia and Venezuela; those of *S. griseicollis* are from the northern sector of the Eastern Andes in Santander and Norte de Santander, Colombia. Data for *S. spillmanni* and *S. parkeri* are from Ecuador and taken from Krabbe et al. (2005). See Appendix A for a list of specimens examined.

Species	Body mass	Wing (flat)	Tail	Tarsus	Bill length[a]	Bill height[b]	Bill width[b]
S. perijanus	17.7 (16.5–20.5) $n = 10$	57.4 (51.5–65.0) $n = 32$	40.3 (32.0–48.0) $n = 32$	21.1 (19.4–22.4) $n = 32$	6.8 (5.7–8.3) $n = 32$	3.5 (3.0–3.9) $n = 27$	2.9 (2.1–3.4) $n = 32$
S. latebricola	23.8 (21.5–26.0) $n = 3$	62.5 (59.5–66.5) $n = 14$	42.3 (39.1–45.3) $n = 12$	23.4 (22.4–24.4) $n = 14$	7.8 (6.9–8.9) $n = 13$	4.1 (3.7–4.7) $n = 11$	3.2 (2.6–3.7) $n = 14$
S. meridanus	15.3 (13.5–16.5) $n = 6$	54.0 (50.0–57.0) $n = 13$	39.9 (35.0–46.0) $n = 13$	21.2 (19.3–22.6) $n = 13$	6.0 (5.5–6.6) $n = 13$	3.1 (2.8–3.5) $n = 12$	2.5 (2.1–2.6) $n = 12$
S. caracae	—	55.9 (53.0–60.0) $n = 16$	40.4 (37.0–47.0) $n = 16$	22.0 (20.8–23.1) $n = 16$	7.0 (6.5–7.4) $n = 16$	3.5 (3.2–3.8) $n = 16$	2.8 (2.5–3.0) $n = 16$
S. griseicollis	16.6 (15.0–18.5) $n = 15$	58.0 (52.0–61.0) $n = 17$	41.4 (36.0–44.7) $n = 15$	21.2 (19.5–22.2) $n = 17$	7.1 (6.3–7.9) $n = 16$	3.3 (3.0–3.7) $n = 14$	3.2 (2.8–3.6) $n = 17$
S. spillmanni	25.2 (21.0–30.0) $n = 36$	61.9 (56.0–67.0) $n = 38$	45.3 (39.0–54.0) $n = 35$	24.5 (22.2–26.0) $n = 18$	7.0 (6.1–7.6) $n = 14$	—	—
S. parkeri	22.5 (21.0–24.4) $n = 13$	62.9 (59.0–66.0) $n = 14$	44.5 (42.3–50.0) $n = 13$	24.6 (23.8–25.3) $n = 14$	6.4 (6.1–7.0) $n = 8$	—	—

[a] From fore edge of operculum to tip
[b] At fore edge of operculum

Diagnosis: Plumage Coloration and Morphology

The new species exhibits all the characteristics of the genus *Scytalopus* (Ridgway 1911, Krabbe and Schulenberg 1997, Cuervo et al. 2005, Maurício et al. 2008). In plumage coloration, the new species is most similar to the population of *S. griseicollis* of the middle sector of the Eastern Andes, but adult males and females exhibit a brown nuchal patch that contrasts with a gray back. Also, all sexes and ages exhibit a variable extent of buff feathers in the lower belly. In comparison to the northernmost populations of *S. griseicollis* (heretofore referred to as northern *S. griseicollis*) from the Tamá massif to the western slope in northern Santander (Zimmer 1939, Donegan and Avendaño 2008), the new species is duller gray, and its upperparts are not extensively brown. *Scytalopus perijanus* is also similar to *S. caracae* and *S. meridanus* but is duller ventrally than *S. caracae* and has a gray back, not brown as in *S. meridanus*. Also, males of the new species tend to be larger in body and bill size than *S. meridanus* (Table 1). Compared to *S. latebricola*, *S. perijanus* can be distinguished by its decidedly brighter plumage, smaller size, shorter tarsus, and smaller bill (i.e. shorter in length and height). Compared to *S. atratus* and *S. sanctaemartae*, the new species lacks a white coronal patch, its dorsal plumage is lighter grayish brown instead of blackish gray or black, it has no whitish tips to any of the ventral feathers, and it has a darker throat. The new species is distinguishable from *S. spillmanni* and *S. parkeri* by its lighter plumage and smaller size (Table 1), and it is lighter in plumage coloration than *S. latrans*, with a buffy belly and extensive brown in the rump and flanks. Nestlings and fledglings of *S. perijanus* appear to be distinguishable from those of northern *S. griseicollis* by their mostly yellowish instead of whitish appearance and by a blacker barring; in *S. meridanus*, barring in juveniles is less yellowish and darker brown than in *S. perijanus*.

Diagnosis: Vocalizations

Scytalopus perijanus is diagnosable by its vocalizations from other *Scytalopus* taxa in multiple temporal and spectral traits. The primary song of *S. perijanus* is a short "churr" delivered in a series of 2 and up to 65 repeats at 0.5–3.0 s intervals (Figure 1). Each song churr (0.8 ± 0.2 s, 11.9 ± 1.5 notes) is distinguishable from the much longer and richer songs of *S. meridanus* (20.9 ± 7.5 s, 169.8 ± 38.6 notes), *S. latebricola* (9.9 ± 2.3 s, 117.0 ± 45.4 notes), and northern *S. griseicollis* (1.5 ± 0.2 s, 34.6 ± 5.5 notes). The song pace (notes s^{-1}) in *S. perijanus* (14.7 ± 2.1; Figure 2A) is similar to that of *S. meridanus* (9.5 ± 5.0; Figure 2C), but it is faster than in *S. latebricola* (11.5 ± 2.3; Mann-Whitney test: $U = 8$, $p < 0.05$; Figure 2B) and slower than northern *S. griseicollis* (23.7 ± 0.9; $U = 0$, $p < 0.01$; Figure 2D). Compared to *S. caracae* and *S. atratus*, the new species songs are distinct in multiple characteristics (Figures 2E, 2F). On spectral traits, *S. perijanus* can be distinguished from northern *S. griseicollis* by a higher minimum frequency (2.7 ± 0.3 vs. 1.7 ± 0.5 kHz), maximum frequency (3.8 ± 0.2 vs. 2.1 ± 0.5 kHz), peak frequency (3.4 ± 0.2 vs. 1.9 ± 0.5 kHz), and bandwith (frequency range; 1.1 ± 0.2 vs. 0.4 ± 0.1 kHz; $U = 0$, $p < 0.01$), and from *S. latebricola* by a lower maximum frequency (3.8 ± 0.2 vs. 4.2 ± 0.2 kHz; $U = 4$, $p < 0.01$). Apparent differences in maximum frequency and bandwith with respect to *S. meridanus* (see Discussion) were not significant based on our sample ($U = 19$, $p = 0.56$); however, *S. perijanus* lacks the high-pitched and introductory notes often included in the songs of both *S. meridanus*

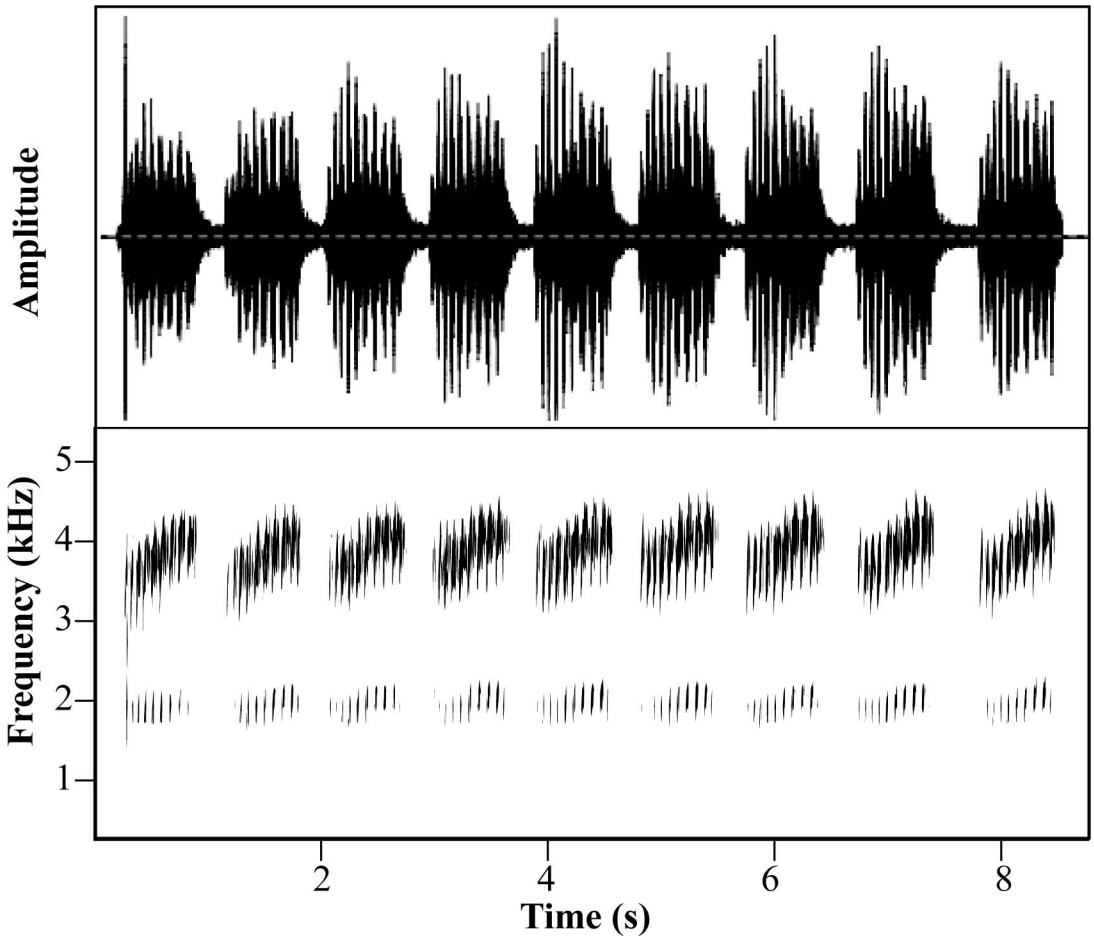

FIGURE 1. Waveform (above) and spectogram (below) depicting the relative amplitude and frequency, respectively, of an excerpt of 9 churr phrases of the primary song of *S. perijanus* sp. nov. recorded at San Antonio, above Manaure, Cesar, Colombia, February 2009 (CSA 2804).

and *S. latebricola*. In addition, the song of *S. perijanus* is mainly formed by upstroke notes (as in *S. latebricola*), unlike the mostly downstroke or short unmodulated notes of *S. meridanus*, and the up-down strokes of *S. caracae* and northern *S. griseicollis* (Figure 2).

The call of *S. perijanus* is short (0.8 ± 0.1 s) and fast-paced (23.7 ± 1.4 notes s^{-1}; Figure 3A); the pace is faster than in *S. latebricola* (20.7 ± 1.6 notes s^{-1}; $U = 23$, $p < 0.001$; Figure 3B) and *S. meridanus* (18.3 ± 1.5 notes s^{-1}; $U = 0$, $p < 0.001$; Figure 3C), but slower than in northern *S. griseicollis* (29.3 ± 1.9 notes s^{-1}; $U = 0$, $p < 0.01$; Figure 3D). It is also shorter than in *S. meridanus* (1.3 ± 0.2 s; $U = 0$, $P < 0.001$) and has fewer notes than in northern *S. griseicollis* (18.9 ± 1.6 vs. 27.2 ± 5.7; $U = 9.5$, $p < 0.001$). Additionally, the call of *S. perijanus* can be distinguished from calls of *S. latebricola* and northern *S. griseicollis* by having lower and higher frequency traits, respectively, as follows: maximum frequency (4.6 ± 0.2 vs. 6.2 ± 0.5 and 3.2 ± 0.2 kHz), minimum frequency (3.4 ± 0.1 vs. 4.5 ± 0.4 and 2.5 ± 0.2 kHz), bandwith (1.3 ± 0.1 vs. 1.7 ± 0.5 and 0.7 ± 0.1 kHz), and peak frequency (4.1 ± 0.2 vs. 5.2 ± 0.5 and 2.9 ± 0.2 kHz; $U = 0$, $p < 0.001$ for all comparisons; Figure 3B–3D). However, the calls of *S. meridanus* and of the new species seem not to differ in spectral traits. The call of *S. perijanus* is clearly distinguishable from those of *S. caracae*, *S. spillmanni*, *S. parkeri*, and *S. atratus* in numerous vocal traits (Figure 3E–3H). Likewise, alternative and advertising songs are distinctive from those known for other *Scytalopus* (see Discussion). Distinctiveness of vocal signals across *Scytalopus* matches phylogenetic clusters (Arctander and Fjeldså 1994, Cuervo et al. 2005, Maurício et al. 2014; see Discussion: Systematics); therefore, the new species is diagnosable morphologically, vocally, and also genetically.

Description of Holotype

The holotype is a fairly small tapaculo (18.5 g) with 8 rectrices. Lores, forehead, crown, auriculars, mantle, and scapular area are Dark Neutral Gray 83 (color nomenclature and numbers follow Smithe 1975, 1981). Feathers in

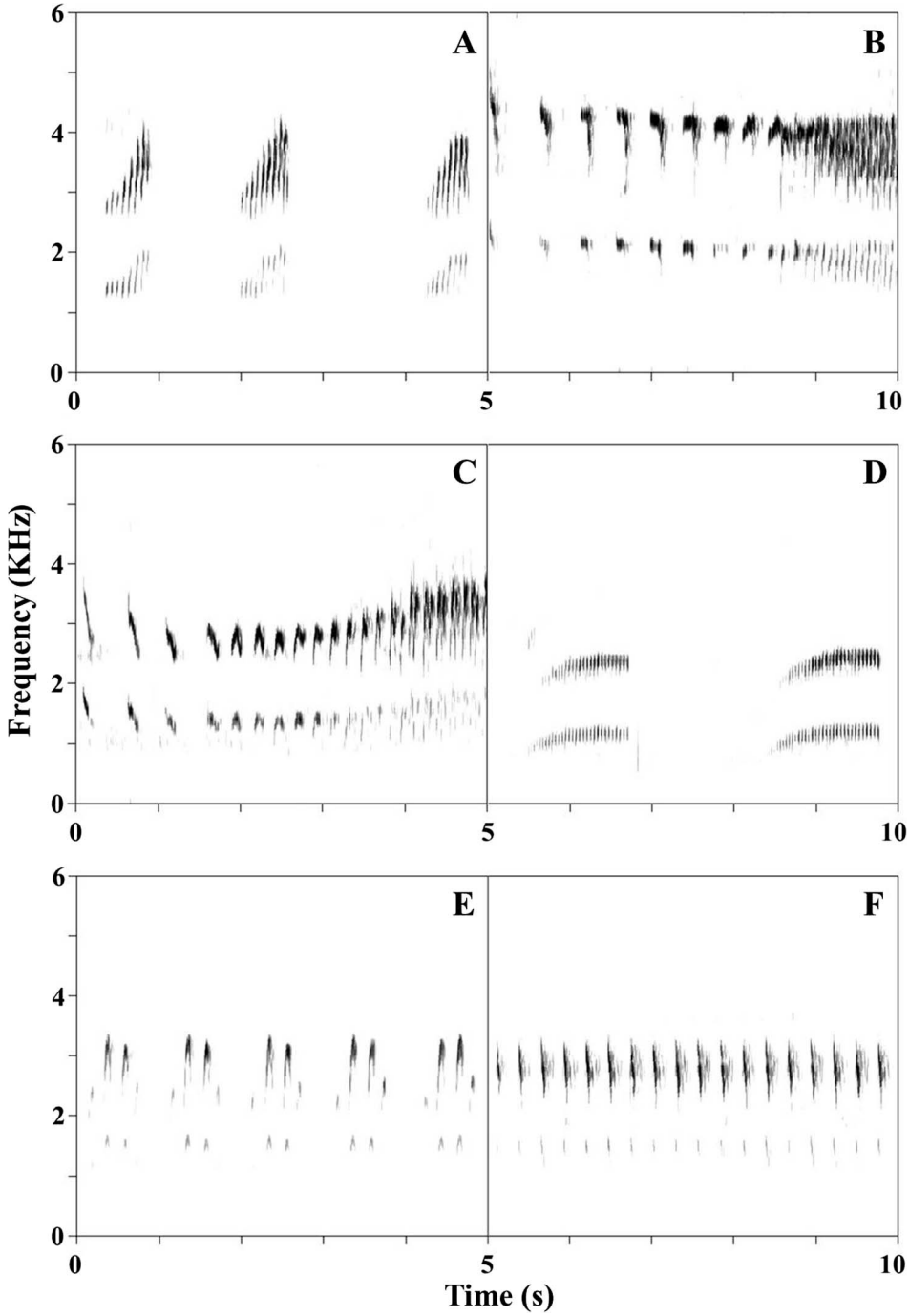

FIGURE 2. Sonograms of fragments of the primary song of *Scytalopus perijanus* sp. nov. and other northern species in the genus. (**A**) Three bouts by *S. perijanus*, type locality, February 10, 2009 (CSA 2803); (**B**) *S. latebricola*, Santa Marta, Magdalena, Colombia, February 12, 2007 (Krabbe 2008); (**C**) *S. meridanus*, 10 km SE La Azulita, Mérida, Venezuela, February 18, 1985 (XC 6236, C. Parrish); (**D**) reeling song of northern *S. griseicollis*, California, Santander, Colombia, June 16, 2009 (J. E. Avendaño); (**E**) *S. caracae*, Colonia Tovar, Aragua, Venezuela, October 11, 2005 (XC 3800, N. Athanas); (**F**) *S. atratus* cf. *nigricans*, Tamá N. P., Norte de Santander, Colombia, August 1999 (Álvarez et al. 2007).

the scapular area have inner webs tinged between Dark Neutral Gray 83 and Verona Brown 223B whereas outer webs are Dark Neutral Gray 83. The color of the nape is between Verona Brown 223B and Dark Drab 119B. Back and rump fall between Verona Brown 223B and Amber 36, with some feathers of the back Dark Neutral Gray 83. Upper-tail coverts are Mars Brown 223A and, like the rump, barred with Sepia 219. Chin, throat, breast, and

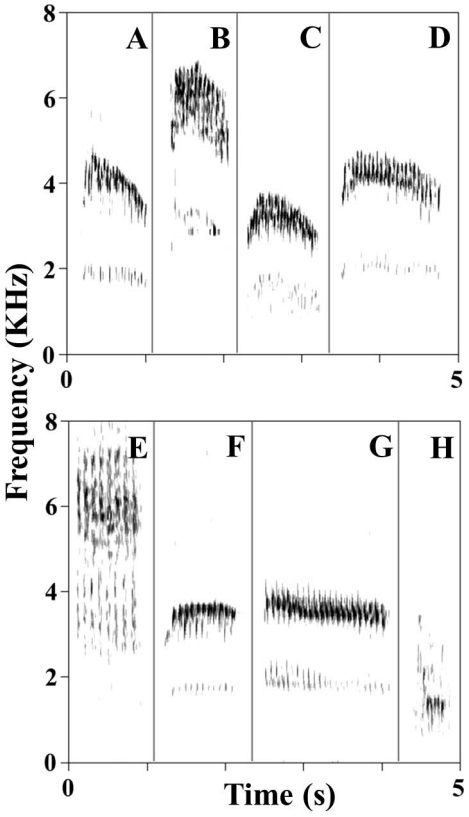

FIGURE 3. Sonograms of calls of *Scytalopus perijanus* sp. nov. and other northern species in the genus. (**A**) *S. perijanus*, Sabana Rubia, Manaure, Cesar, Colombia, July 6, 2008 (CSA 2810); (**B**) *S. latebricola*, San Lorenzo, Santa Marta, Magdalena, Colombia, February 12, 2007 (Krabbe 2008); (**C**) *S. meridanus*, Loma Redonda-La Aguada, Sierra Nevada N. P., Mérida, Venezuela, February 18, 2000 (XC 50486, B. López-Lanús); (**D**) northern *S. griseicollis*, California, Santander, Colombia, June 6, 2009 (XC 86713, J. E. Avendaño); (**E**) *S. caracae*, Cortada de Maya road, Colonia Tovar, Aragua, Venezuela, October 11, 2005 (XC 3801, N. Athanas); (**F**) *S. spillmanni*, Finca Andalucía, San Vicente del Caguán, Caquetá, Colombia (Álvarez et al. 2007); (**G**) *S. parkeri*, Acanamá, Loja, Ecuador, February 13, 1991 (XC 32893, N. Krabbe); (**H**) *S. atratus confusus*, Bosque Las Ánimas, Amalfi, Antioquia, Colombia (Álvarez et al. 2007).

center of belly are between Medium Neutral Gray 84 and Light Neutral Gray 85. Sides of breast are Dark Neutral Gray 83, whereas the lower breast and center of belly are washed with whitish (close to Pale Neutral Gray 86). Lower belly and flanks are between Clay 123B and Tawny 38. Thighs and under-tail coverts are between Verona Brown 223B and Amber 36, and indistinctly barred blackish. Rectrices and remiges are Vandyke Brown 121. Margin of tertials and the tip of the outer web are Mikado Brown 121C. Under-wing coverts are Clay 123B. The tip of the 3 external rectrices has a terminal band between Verona Brown 223B and Amber 36 and a subterminal band of Sepia 219. Soft parts in life: irides dark brown; bill dull horn with maxillary tip and mandibular tomia paler; tarsi brown with frontal side and toes whitish brown; claws whitish to grayish bone, hind claw gray; and foot soles pale yellow. The holotype had abundant subcutaneous fat and light molt in crown, mantle, and throat, and the sixth right primary was sheathed. Stomach contained insect remains. Testes were enlarged (left testis: 7.2 × 4.3 mm; right testis 5.4 × 3.2 mm). Measurements (in mm): bill (from tip to fore edge of operculum) length: 6.8; bill height: 3.4; bill width: 3.2; tarsus: 20.3; tail: 44.6; wing (flattened) 61.2 mm.

Paratypes

We designate as paratypes a series of 16 round-skin specimens at ICN and IAvH-A collected in 2008 and 2009. Eleven were taken at the type locality between ~2,450 m and 2,600 m: adult males: ICN 36732, 36798, 36766; adult female: ICN 36729; subadult males: ICN 36799, 37069, 37091, 37101; fledgling males: ICN 36734, 36800; fledgling female: ICN 36801. The remaining 4 paratypes were collected upslope in paramo vegetation at Sabana Rubia, a few kilometers from the Venezuela border, Municipality of Manaure, Department of Cesar, Colombia (10°22′01″N, 72°53′51″W, ~3,025 m): adult males: ICN 36838, IAvH-A 15290; adult female: ICN 36857; fledgling female: ICN 36852.

Etymology

The Latin, English, and Spanish names refer to the Serranía de Perijá of Venezuela and Colombia, the mountain range to which the new bird species is endemic.

DISCUSSION

Variation Within the Type Series

Phenotypic variation in the type series is associated with age and sex and mainly involves the degree of dullness in the underparts, the extent of buffy coloration in the belly, and the presence and extension of a brown nuchal patch. Adult males are similar ventrally to the holotype, although 2 are duller (ICN 36766 and 36798) and another one is paler (i.e. light gray, ICN 36732). Only one male specimen (ICN 36798) exhibits a nuchal patch resembling that of the holotype. Two specimens (ICN 36838 and 36839) have a gray nuchal patch tinged with Verona Brown, which is hardly visible in 3 males (ICN 36732, 36766, and 36799). Color variation in the flanks and under-tail coverts is subtle, but 3 adult males (ICN 36760, 36798, and 36838) are slightly duller than the holotype. Coloration of the lower belly appears to be invariant across male specimens.

In females, the nuchal patch is more conspicuous than in adult males, between Verona Brown 223B and Raw Sienna 136 (Figure 4). The underparts resemble that of the type and other adult male specimens but have a lighter lower-breast mixed with Pale Pinkish Buff 121D reaching the lower belly (e.g., ICN 36729) or the upper belly (e.g., ICN 36857). Subadult males have a light gray washing in the belly, tinged

FIGURE 4. Female (left) and male (right) Perijá Tapaculo *Scytalopus perijanus* sp. nov. attending a nestling (center). Note the more rufous nuchal patch in the female. Watercolor by Jon Fjeldså.

with Pale Neutral Gray 86 (ICN 37091) or with Clay color 123B (ICN 37069). The nuchal patch is barely evident in 2 subadult birds (ICN 37091 and 37101) but is conspicuous in another (ICN 37069), in which the nuchal patch extends to the upper back, presumably a retention of juvenile plumage.

Like in the holotype, the back of adult males, females, and one subadult male (ICN 37069) is gray mixed with brown, but in 2 subadult males (ICN 37101 and 37091) the back is uniform gray. Rump coloration is slightly tawnier in one female (ICN 36857) and in subadult males. The extent of brown in secondaries is also variable, in some cases restricted to feather tips as in one adult male (ICN 36732) and immature males, or covering half of each feather (e.g., adult male ICN 36838) or all the feather (female ICN 36857).

Regarding fledgling plumage, the male (ICN 36734) has more densely barred upperparts between Verona Brown 223B and Mikado Brown 121C than the female (ICN 36852), which lacked any barring in the head and back; this suggests that the female fledgling specimen was older than the male fledgling. In general, light to moderate body molt and light symmetric molt in wings and tail feathers were present in adult specimens, and one subadult male (ICN 37069) still had first-year secondary feathers. The number of rectrices is variable in the type series (range 8–12), but 5 of 7 adult males have 12.

Additional Specimens Examined

We examined 140 specimens of 5 *Scytalopus* taxa, including 45 additional specimens we identified as *S. perijanus* (Appendix A). The historical specimens of *S. perijanus*, including Carriker's series, exhibit variation within the range observed in the type series.

Systematics

We used DNA sequence data from 3 *S. perijanus* specimens (ICN 36729, 36734, and 36766) to provide a hypothesis of the systematic affinities of the new species with respect to the other *Scytalopus* with which it has been confused in the literature, namely *S. caracae*, *S. latebricola*, *S. griseicollis*, *S. meridanus*, and *S. atratus*. In addition, we assessed genetic divergence among these species and others occurring in northern Colombia and Venezuela. Sequences of the ND2 mitochondrial gene were generated for an ongoing diversification analysis of the genus with nearly complete taxon sampling and dense geographic coverage across the Northern Andes (C. D. Cadena et al. personal communication). We used sequences of 3 scytalopodinae tapaculos as outgroups: *S. novacapitalis*, *Myornis senilis*, and *Eleoscytalopus indigoticus* (Maurício et al. 2008). We truncated the original alignment in reference to an 843-bp sequence of *S. caracae* obtained from a toe pad sample (COP-IC1209). New sequences were deposited in GenBank (accession nos. KM668104-KM668115); specimens used in the analysis are highlighted in Appendix A.

Ongoing phylogenetic studies of *Scytalopus* indicate that *S. perijanus* belongs in a clade including several species from the Northern Andes largely corresponding to the *latebricola* group (sensu Zimmer 1939) plus a few recently described species (C. D. Cadena et al. personal communication). All the taxa considered here, with the exception of *S. atratus* and outgroups, also belong to this clade. We estimated the ND2 gene tree for our study taxa implementing a Bayesian analysis in MRBAYES, v3.1.2 (Huelsenbeck and Ronquist 2001). Four independent analyses consisting of 4 MCMC chains were run for 10 million steps, of which 25% were discarded as burn-in. The best-fit substitution model (GTR+I) according to the Akaike's information criterion calculated using MRMODELTEST v2.3 (Nylander 2004) was implemented in the analysis. In addition, we conducted a maximum-likelihood (ML) analysis in RAxML, v7.2.6 (Stamatakis 2006), which implemented the GTR+Γ model.

Our analyses indicated that the closest relatives of *S. perijanus* are *S. meridanus*, *S. caracae*, and *S. latebricola* (Figure 4), but they were unable to determine its sister species, possibly as a result of rapid diversification. The new species and the 3 species mentioned above form a clade sister to *S. griseicollis* (Figure 5). Uncorrected genetic distances between *S. perijanus* and its 3 closest relatives

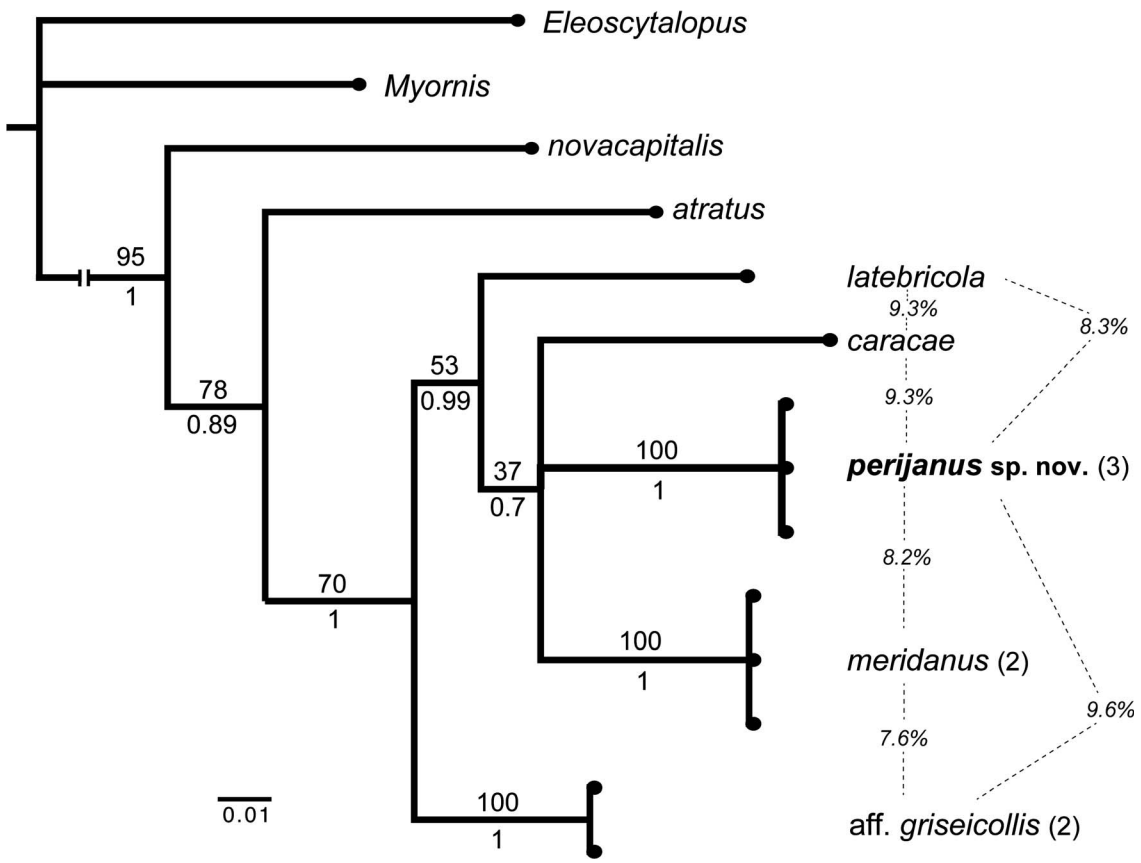

FIGURE 5. Phylogenetic position of *S. perijanus* sp. nov. within a clade of tropical montane *Scytalopus* from northern South America based on ND2 sequences. The phylogeny is a 50% majority-rule consensus tree from the Bayesian analysis. Numbers at nodes represent Bayesian posterior probabilities (below) and maximum-likelihood bootstrap support values (above). Numbers in front of species names are the number of individuals sequenced per species (Appendix A). Genetic distances between species (uncorrected-*p*) are shown as percentages.

ranged from 8.2% to 9.3%, which exceeds divergence between some closely related species of Andean tapaculos (Cuervo et al. 2005, Krabbe and Cadena 2010) and is similar to the divergence among species in the *speluncae* group (Mata et al. 2009, Maurício et al. 2014). These levels of divergence suggest a long period of evolutionary isolation, which is not unusual in lineages of cloud forest birds endemic to the Serranía de Perijá and adjacent ranges (Cadena and Cuervo 2010, Derryberry et al. 2011, Benham et al. 2015, Valderrama et al. 2014).

Vocalizations

We analyzed 9 vocal variables of primary songs and calls to assess vocal divergence of *S. perijanus* and 3 geographically adjacent *Scytalopus* taxa, including 2 of its closest relatives (*S. latebricola*, *S. meridanus*, and northern *S. griseicollis*). Songs of the more geographically isolated *S. caracae* were not analyzed, but previous descriptions (Fjeldså and Krabbe 1990, Krabbe and Sculenberg 1997) demonstrated that its vocalizations differ drastically from those of any other tapaculo. For each vocalization, we measured ~60% of notes, sampling equal proportions (20%) at the beginning, middle, and end of the vocalization, using the program Raven Pro v1.3 (Charif et al. 2008) in blackman window type, with a resolution of 512 bands and overlap of 99%. We analyzed the following variables for each vocalization (single calls and song churrs): number of notes, song length, note pace, note length, interval length between notes, minimum frequency, maximum frequency, bandwidth, and peak frequency. We analyzed 4–9 different individuals per species and measured and averaged 1–4 vocalizations per individual (Appendix B). We determined whether taxa were vocally distinguishable in multivariate space using discriminant analyses based on 8 quantitative variables (i.e. excluding number of notes). Alternative and advertising songs (Krabbe and Schulenberg 1997) were qualitatively compared and described.

Discriminant analysis based on average values demonstrated that *S. perijanus*, *S. latebricola*, *S. meridanus*, and northern *S. griseicollis* are distinguishable in multivariate space in primary songs (Wilks's $\lambda = 0.002$, $F = 112.9$, $p < 0.001$, $n = 24$ individuals) and calls (Wilks's $\lambda = 0.003$, $F =$

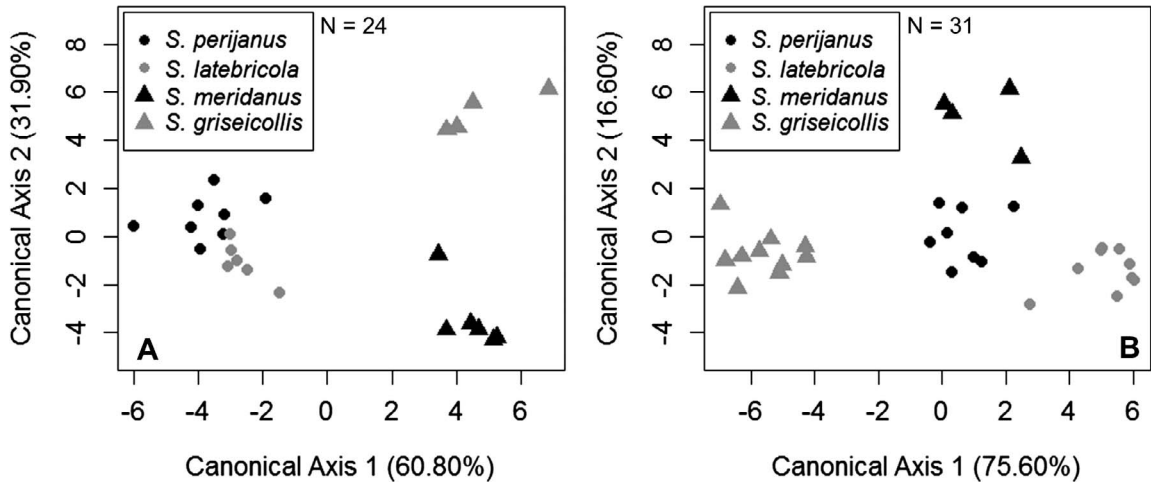

FIGURE 6. Multivariate space of vocal signals of *S. perijanus* sp. nov. and other 3 related species from the first 2 functions of discriminant analysis based on 8 quantitative acoustic variables taken on primary songs (**A**) and calls (**B**). Values for primary songs and calls are from different individuals; each one represents one vocalization or the average of 2–4 vocalizations per individual (Appendix B).

145.8, $p < 0.001$, $n = 31$ individuals). All vocalizations were assigned to their corresponding species (Figure 6). Primary songs were best discriminated by the canonical function 2 (CF 2), which was associated with all variables except note length. Bandwidth was the only uninformative variable across analyses. Calls were discriminated by frequency variables along CF 1 and by pace and song length along CF 2 (Table 2).

The alternative song of *S. perijanus* (Figure 7A) was analyzed based on recordings of 5 different individuals. This song type is elicited as a response to playback or during agonistic encounters, presumably by males, while perching 1.0–1.5 m above ground. It consists of a series of 11–22 accelerating churrs, mostly delivered every 0.1–0.9 s. The first 2–3 churrs of each song consist of 4–5 notes where the first note is flat and the rest are upstrokes. Then, gradually, the churrs reach 9–14 up-down strokes, rarely up to 90 notes. This vocalization may be emitted in ascending or descending pitch, reaching a peak at 3.7–4.5 kHz. The alternative song of *S. latebricola* has similar pitch to that of *S. perijanus* (Figure 7B) but consists of fewer (2–7) churrs. The first churr in *S. latebricola* has 7–13 notes; the following churrs seem to have more notes on average, and these are up-strokes. In songs composed of 2 churrs, the last one may extend to up 70 notes in *S. latebricola*. To our knowledge, no recordings of alternative songs are available for *S. griseicollis*, *S. meridanus*, or *S. caracae*.

TABLE 2. Results of discriminant analysis based on 7 acoustic measurements of primary songs and calls of 4 *Scytalopus* species from the Northern Andes: *S. perijanus* sp. nov., *S. latebricola*, *S. meridanus*, and *S. griseicollis*. The acoustic variables that contributed significantly to the first 2 canonical functions (CF) are highlighted in bold. The cumulative variance explained by the first 2 CF was 92.7% and 92.2% for songs and calls, respectively. Delta frequency is not included because this variable did not contribute to the canonical functions.

	Primary songs		Calls	
Acoustic variable	CF 1	CF 2	CF 1	CF 2
Song length	0.284	**−0.618**	−0.063	**0.380**
Pace	0.078	**0.543**	−0.513	**−0.536**
Note length	−0.141	**−0.239**	0.356	0.284
Interval length between notes	0.143	**−0.343**	0.199	0.361
Low frequency	−0.190	**−0.375**	**0.644**	−0.134
High frequency	−0.292	**−0.639**	**0.815**	−0.208
Peak frequency	−0.303	**−0.611**	**0.658**	−0.162
Variance explained	60.80%	31.90%	75.60%	16.60%

An advertising song similar to that of females of several other species of *Scytalopus*, including *S. spillmanni*, is given by *S. perijanus*, presumably by females (Figure 7C, 7D). Our single recording was a series (~9.5 s long) of 32 explosive up-down strokes. The first 4 notes were delivered in pairs and were high-pitched (4.7–5.7 kHz). From the fifth note on, notes were single, and the pitch gradually descended to 5.1 kHz at the 24th note, increasing again at the end to 5.4 kHz. Time intervals between notes decreased gradually from 0.63 s (between the first and second note) to 0.08–0.16 s. The female advertising song of *S. spillmanni* is apparently lower-pitched on average, slightly slower (3.0 vs. 3.4 notes s^{-1}), and composed only of single notes.

Distribution

Scytalopus perijanus has been recorded at 19 localities on both slopes of the Serranía de Perijá (Appendix C). On the Venezuelan slope, it is known from 9 localities, ranging in elevation from 1,800 (at Cerro Tetarí, La Teta or Las Tetas and Las Antenas, Río Negro, Zulia; Lentino

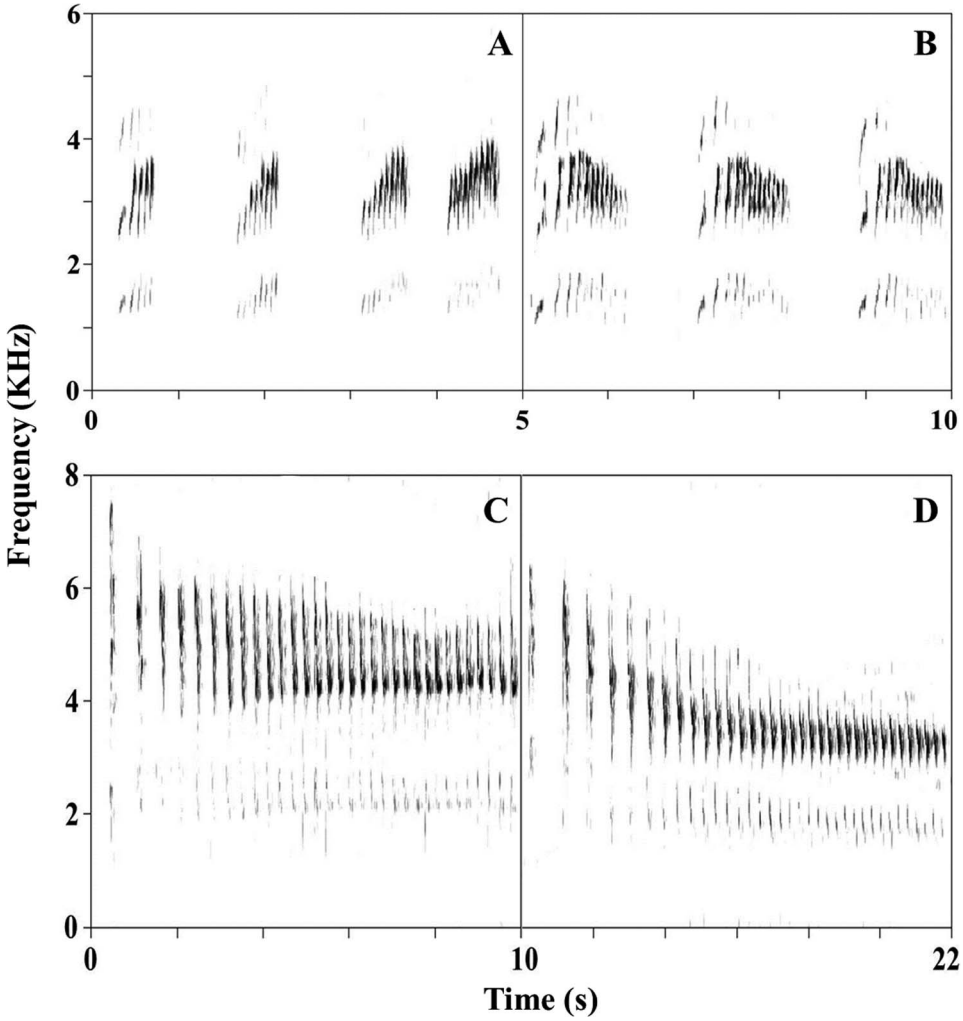

FIGURE 7. Introductory churrs of alternative songs delivered after stimulation with playback: (**A**) *S. perijanus* sp. nov., Sabana Rubia, Manaure, Cesar, Colombia, July 6, 2008 (CSA 2818); (**B**) *S. latebricola*, Nabusamike, Cesar, Colombia, February 19, 2007 (Krabbe 2008). Advertising songs: (**C**) *S. perijanus* sp. nov., type locality, July 6, 2008 (CSA 2822); (**D**) *S. spillmanni*, Ucumarí N. P., Risaralda, Colombia, July 17, 2001 (Álvarez et al. 2007).

et al. 2004) to 3,120 m (at Cerro Tetarí). On the Colombian slope, *S. perijanus* is known from 10 localities in departments of La Guajira and Cesar ranging from 1,600 m (below San Antonio, above Manaure, Cesar) to 3,225 m (Cerro Pintado, La Guajira). However, the lower elevational limit remains to be established owing to the scarcity of fieldwork and to the extensive deforestation below 1,600–2,000 m.

Scytalopus tapaculos often exhibit elevational replacements with habitat seggregation where their ranges meet. It is likely that only 2 species occur in Serranía de Perijá, as in the adjacent Sierra Nevada de Santa Marta where an *atratus* lineage (i.e. *S. sanctaemartae*) occurs in the foothills and mid elevations and *latebricola* occurs in the highlands. *Scytalopus perijanus* has not been recorded in sympatry with any other *Scytalopus* species. It is possible, however, that its range overlaps at mid elevations (1,500–1,900 m) with that of *S. atratus nigricans*, which occupies a different microhabitat, and it is only known in the Serranía de Perijá from the east slope (contra Carriker 1954, Meyer de Schauensee 1959) on the basis of 2 specimens taken at 1900 m (Phelps and Phelps 1953, Hilty 2003). However, *S. perijanus* might co-occur with the northern populations of *S. griseicollis* (Donegan and Avendaño 2008) at the low-elevation range of Serranía de los Motilones, which may harbor adequate habitat patches for both species; northern *S. griseicollis* has been collected as far north as the Ocaña range at La Palmita, Norte de Santander. Other species not yet recorded in Serranía de Perijá (López-O. et al. 2014) include *S. sanctaemartae* and *S. latrans*, but they occur in adjacent mountain regions at lower elevations and in different habitats from those of the new species.

To better assess the potential distribution of *S. perijanus*, and ultimately its conservation status, we conducted an ecological niche modeling (ENM) analysis in Maxent v3.3 (Phillips et al. 2006) using 19 climate variables (Hijmans et al. 2005), and 13 remote-sensing variables related to vegetation and 3 related to topography (Buermann et al. 2008). We used all the localities reported in this paper to build the model (Appendix C). The distribution model suggests that *S. perijanus* is potentially restricted to the northern section of the Serranía of Perijá between 10°51′N and 09°42′N, apparently tracking the distribution of humid vegetation above 1,600 m including elfin forests and paramo habitats (Figure 8). However, the species might be found further south in the Serranía de los Motilones. Fieldwork is necessary along the Motilones in southern Cesar and northern Norte de Santander in Colombia and southwestern Zulia in Venezuela to evaluate distributional limits of the new species and other *Scytalopus* tapaculos occurring in the region.

Breeding Biology

The reproductive biology of *Scytalopus* tapaculos is poorly known (Krabbe and Schulenberg 2003, Greeney 2008). We found and collected a nest of *S. perijanus* (ICN-N-231) on July 13, 2008, within a 2–3 m tall secondary forest patch close to the forest edge, 2 m from the dirt road that crosses the type locality. Nest location was facilitated by the loud cricket-like calls elicited by 2 nestlings (ICN 36800, 368001) and the ejection of fecal sacs. An individual that approached the nest was an adult male (ICN 36798) with enlarged testes and no molt, which indicates male participation in parental care as documented for other *Scytalopus* (Greeney et al. 2005, Decker et al. 2007, Freeman and Greeney 2008, Hosner and Huanca 2008).

Following the terminology of Simon and Pacheco (2005), the nest was a subterranean cavity with a short tunnel entrance connected to the chamber, which was closed and had a globular shape, mainly made of mosses, grasses, and plant rootlets. Dimensions were 12 cm in diameter, 9 cm width, and 14.5 cm depth. The entrance was ~4.2 cm diameter by 10 cm deep and was partially covered by some stems and leaves of *Pteridium aquilinum* (Dennstaedtiaceae), *Huperzia* sp. (Lycopodiaceae), *Sphagnum* sp. (Sphagnaceae), *Alloispermum caracasanum* (Asteraceae), *Geranium* sp. (Geraniaceae), and *Lachemilla* sp. (Rosaceae). The area surrounding the nest was humid with a high density of shrubs and small trees, mainly *Tibouchina* sp. (Melastomataceae), *Cleome* sp. (Cleomaceae), and *Achyrocline alata* (Asteraceae). There were also representatives of *Baccharis prunifolia*, *Ageratina cuatrecasasii* (Asteraceae), *Relbunium* sp. (Rubiaceae), *Sphagnum* sp., and *Solanum* sp. (Solanaceae) among the leaf litter neighboring the nest.

The nest architecture and clutch size of *S. perijanus* are similar to those reported for other species in the genus, including *S. griseicollis* (Krabbe and Schulenberg 2003), *S. parkeri* (Greeney and Rombough 2005, Greeney 2008), *S. spillmanni* (Pulgarín-R. 2007), *S. meridanus* (Decker et al. 2007), and *S. parvirostris* (Smith and Londoño 2014). Loud begging calls of *Scytalopus* nestlings have been reported for other species (Skutch 1972, Freeman and Greeney 2008) and have also been described as rapid trills or insect-like in *S. latrans* (Skutch 1972), *S. argentifrons* (Young and Zuchowski 2003), *S. micropterus* (Greeney and Gelis 2005), and *S. parkeri* (Greeney and Rombough 2005).

Our field observations and data taken from specimens suggest that *S. perijanus* probably breeds from April to July. In early May 1942, Carriker collected a laying female, and several males and females collected from May to June had enlarged gonads. Fledglings were collected from the last week of June through July (USNM). This agrees with our finding of fledglings, a nest, and nestlings in July 2008, and with reproductive signals shown by most adults collected at that time (i.e. enlarged gonads, abundant subcutaneous fat, worn plumage, and slight to moderate molt). A specimen collected on February 1951 in Cerro Tamuypejocha on the Venezuelan side is labeled as a juvenile (PONS 2888; Ginés et al. 1953). We did not find juveniles in February 2009 but registered 3 subadult males and noted much lower vocal activity than in July 2008.

Ecology and Behavior

Like many other forest tapaculos, *S. perijanus* is secretive and difficult to see. The species seems to be common in dense interior and forest edges of humid and elfin forests and highland woody bushes in paramo habitat, especially between 2,500 and 3,000 m elevation. At El Cinco (type locality), paramo Sabana Rubia and San Antonio, we found at least 3–4 territorial males in ~2 ha of suitable habitat; males from at least 2 territories at each site were paired. We observed single individuals foraging in dense thickets within 1 m from the ground, often using forest edges and scrubby vegetation along trails (e.g., patches of *Rubus* sp.). At Sabana Rubia, individuals often foraged on the ground, running across grassy open areas between bushes. Stomach contents from 7 individuals consisted exclusively of insect remains.

Habitat

The elevational range of *S. perijanus* covers a variety of habitats from lower montane to upper montane humid forest, elfin forest, subparamo, and paramo. Cloud forests in the Serranía de Perijá, such as those at the type locality, are typically dominated by *Prumnopitys montana*, *Clusia multiflora*, *Ternstroemia meridionalis*, *Podocarpus oleifolius*, *Weinmannia pinnata*, *Illex sessiliflora*, and *Hesperomeles ferruginea* (Rangel-Ch. and Arellano-P. 2007). Annual rainfall averages ~1,230 mm at Manaure, Cesar, and is seasonally bimodal with slightly drier periods from

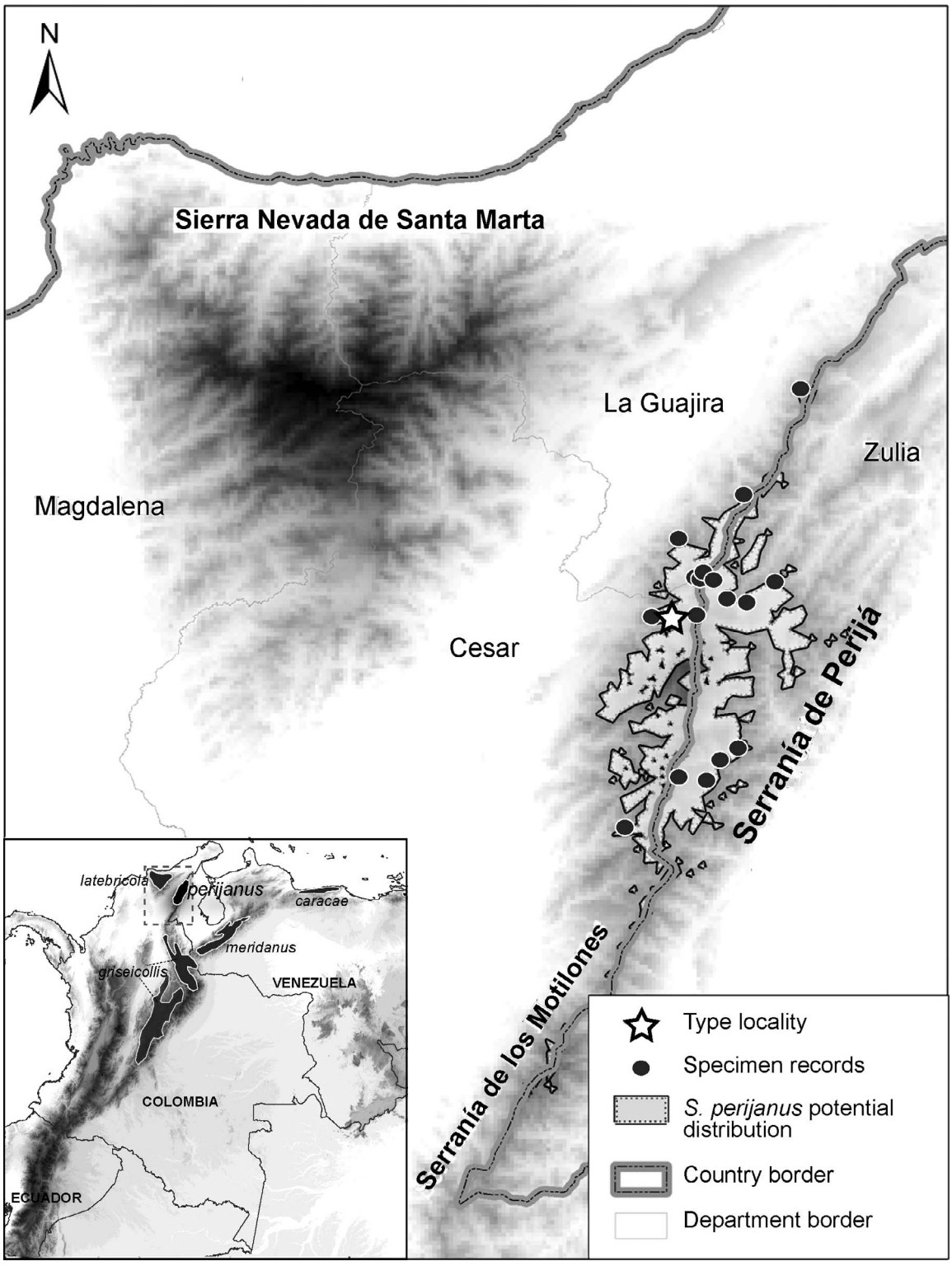

FIGURE 8. Map of northern South America showing the location of areas mentioned in the text, point locality records, and potential distribution of *Scytalopus perijanus* sp. nov. (light gray polygons along the Venezuelan–Colombian border). The projected distribution of the new species was defined as $\geq$0.5 presence probability of the ENM model calculated in MAXENT. Note the restricted range of the new species to the northern sector of the Serranía de Perijá mainly above 1,600 m.

December to April and in July (Arellano-P. et al. 2007). Vegetation at the treeline inhabited by *S. perijanus* is dominated by bushes (*Diplostephium floribundum*), bamboo (*Chusquea scandens*), and short trees (*Hesperomeles ferruginea* and *Gynoxys* spp.). The subparamo vegetation in the area surrounding Sabana Rubia is dominated by bamboo (*Chusquea tessellata*), grasses (*Calamagrostis intermedia* and *C. effuse*), and bushes (*Lourtegia stoechadifolia*, *Arcytophyllum nitidum*, *Gaylusaccia buxifolia*, *Hypericum baccharoides*, and *H. magdalenicum*), with scattered patches of small trees (*Weinmannia pinnata*; Arellano-P. et al. 2007).

Conservation

The forests and paramo of Serranía de Perijá have a long history of anthropogenic disturbance. Forest cover has been almost completely cleared on the Colombian slope from the foothills up to ~2,000 m in La Guajira (Strewe 2004) and especially around the type locality. The remnant forests above 2,600 m and paramo are highly fragmented (Rangel-Ch. 2007). The region as a whole has been historically affected by timber extraction and clearing for pastures, agricultural fields, illicit crops, and aerial fumigations of the latter (Fjeldså et al. 2005). Currently, the main threats to these habitats are cattle raising, fires, and the abandonment of cultivated land at the tree-line, which have led to the replacement of upper-montane and elfin forests by grassland vegetation typical of the paramo, a process affecting ~37% of the upper Andean forest of the Serranía de Perijá (Arellano-P. and Rangel-Ch. 2007). No protected areas exist on the Colombian side of the range, but ~300,000 ha of humid montane forest and paramo habitats are protected in the Venezuelan side by the Sierra de Perijá National Park.

The extent to which *S. perijanus* tolerates anthropogenic forest disturbance and landscape fragmentation is uncertain. Although data on population size or demographic trends are lacking, we consider this species to be fairly common in heterogeneous landscapes with primary and tall secondary forests subject to logging and small shrubby patches near forest remnants, even in areas surrounded by exotic plantations (e.g., *Eucalyptus globulosus*) and agricultural fields (e.g., coffee). However, we did not detect it in the deforested and burned slopes that have turned into tussock grasslands. Although *S. perijanus* likely tolerates some level of landscape fragmentation, it presumably qualifies as Endangered under IUCN criteria (B1b(i,iii); IUCN 2001), and its small and fragmented range ($<$5000 km^2) will probably continue declining in extent and quality.

Implementing effective actions in the Colombian side of Serranía de Perijá is urgent for the conservation of *S. perijanus* and other threatened and little-known birds such as *Metallura iracunda* and *Asthenes perijana*. In addition, this region is home to other endemic taxa that will likely be treated as full species in the near future (e.g., *Grallaria rufula saltuensis*, *Synallaxis unirufa munoztebari*, and *Ochthoeca diadema rubellula*), or which have been overlooked (e.g., *Myiopagis olallai incognita*; Cuervo et al. 2014). The Serranía de Perijá is recognized by its high endemism (Hernández-Camacho et al. 1992, Viloria and Calchi La C 1993, López-O. et al. 2014), with ~60 avian taxa largely restricted to montane forests and paramo habitats and a number awaiting formal description (A. M. Cuervo personal communication). Likewise, 69 taxa of vascular plants are endemic to this range (Rivera-Díaz and Fernández-Alonso 2003). Establishing a large binational protected area, such as the one protecting the Tamá massif, would be possible with the establishment of new national park or a network of reserves in Colombia connected to the Sierra de Perijá National Park of Venezuela.

ACKNOWLEDGMENTS

We thank our local guides and assistants for their hospitality and help with field work. For access to specimens, we are grateful to C. Medina, S. Sierra, and F. Forero (IAvH-A); F. G. Stiles (ICN); J. Dean and C. Ludwig (USNM); M. Lentino, J. Pérez-Emán, and J. Miranda (COP); M. Salcedo (PONS); and J. V. Remsen (LSUMZ). We thank the contributions and support of J. L. Pérez-Emán (Universidad Central de Venezuela) and D. López and J. D. Palacio (IAvH-BT) for the genetic sampling, and F. García for the identification of botanical specimens. S. González-Caro assisted with the map. We are very grateful to J. Fieldså for the painting (Figure 4), and to all the recordists that contributed songs to xeno-canto.org. We thank D. Ascanio, M. Lentino, J. Pérez-Emán, N. Krabbe, F. G. Stiles, T. S. Schulenberg, and anonymous reviewers for information, literature, or comments that improved this manuscript.

Funding statement: This study was supported by The Explorer's Club, the Facultad de Ciencias at Universidad de los Andes, National Science Foundation DDIG grant (DEB-0910285), the Society of Systematic Biologists, the Lewis and Clark Exploration Fund, Grants-in-Aid of Research of the Society of Integrative and Comparative Biology, the Frank M. Chapman Memorial Fund of the American Museum of Natural History, the Alexander Wetmore Memorial Research Fund of the American Ornithologists' Union, and the Louis Agassiz Fuertes Award of the Wilson Ornithological Society, and Idea Wild. The first trip to Perijá by A. Cortés-Diago and J. P. López-O. was supported by Ministerio del Medio Ambiente, Corpocesar, Corpoguajira, Conservación Internacional-Colombia, and Fundacion EcoHabitats. The visitor fellowship program of the Smithsonian Institution supported J. E. Avendaño's visit to USNM. None of our funders had any influence on the content of the submitted or published manuscript, neither require approval of the final manuscript to be published.

Ethics statement: Collecting permits were obtained from Corpocesar (Resolución 0961).

LITERATURE CITED

Álvarez, M., V. Caro, O. Laverde, and A. M. Cuervo (2007). Guía Sonora de los Andes Colombianos. Banco de Sonidos Animales, Instituto Alexander von Humboldt and Cornell Laboratory of Ornithology, Ithaca, NY.

Arctander, P., and J. Fjeldså (1994). Andean Tapaculos of the genus *Scytalopus* (Aves, Rhinocryptidae): A study of modes of differentiation using DNA sequence data. In Conservation Genetics (V. Loeschke, J. Tomiuk, and S. K. Jain, Editors). Birkhauser Verlag, Basel, Switzerland. pp. 205–225.

Arellano-P., H., and J. O. Rangel-Ch. (2007). Caracterización ecológica, oferta ambiental, uso del suelo, transformación y zonificación ambiental. In Colombia Diversidad Biótica V: La Alta Montaña de la Serranía de Perijá (J. O. Rangel-Ch., Editor). Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia. pp. 347–374.

Arellano-P., H., J. O. Rangel-Ch., and A. M. García-M. (2007). Clima y topoclima. In Colombia Diversidad Biótica V: La Alta Montaña de la Serranía de Perijá (J. O. Rangel-Ch., Editor). Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia. pp. 19–41.

Aveledo Hostos, R., and L. A. Pérez Chinchilla (1989). Tres nuevas subespecies de aves (Picidae, Parulidae, Thraupidae) de la Sierra de Perijá, Venezuela y lista hipotética para la avifauna colombiana de Perijá. Boletín Sociedad Venezolana de Ciencias Naturales 43:7–26.

Benham, P. M., A. M. Cuervo, J. A. McGuire, and C. C. Witt (2015). Biogeography of the Andean metaltail hummingbirds: Contrasting evolutionary histories of treeline and habitat-generalist clades. Journal of Biogeography. doi:10.1111/jbi.12452

Buermann, W., S. Saatchi, T. B. Smith, B. R. Zutta, J. A. Chaves, B. Milá, and C. H. Graham (2008). Predicting species distributions across the Amazonian and Andean regions using remote sensing data. Journal of Biogeography 35:1160–1176.

Cadena, C. D., and A. M. Cuervo (2010). Molecules, ecology, morphology, and songs in concert: How many species is *Arremon torquatus* (Aves: Emberizidae)? Biological Journal of the Linnean Society 99:152–176.

Carriker, M. A., Jr. (1954). Additions to the avifauna of Colombia. Novedades Colombianas 1:14–19.

Charif, R. A., A. M. Waack, and L. M. Strickman (2008). Raven Pro 1.3. Cornell Laboratory of Ornithology, Ithaca, NY.

Clements, J. F., T. S. Schulenberg, M. J. Iliff, D. Roberson, T. A. Fredericks, B. L. Sullivan, and C. L. Wood (2014). The eBird/Clements checklist of birds of the world: Version 6.9. http://www.birds.cornell.edu/clementschecklist/download/

Cracraft, J. (1985). Historical biogeography and patterns of differentiation within the South American avifauna: Areas of endemism. Ornithological Monographs 36:49–84.

Cuervo, A. M., C. D. Cadena, N. Krabbe, and L. M. Renjifo (2005). *Scytalopus stilesi*, a new species of tapaculo (Rhinocryptidae) from the Cordillera Central of Colombia. The Auk 122:445–463.

Cuervo, A. M., F. G. Stiles, M. Lentino, R. T. Brumfield, and E. P. Derryberry (2014). Geographic variation and phylogenetic relationships of *Myiopagis olallai* (Aves: Passeriformes; Tyrannidae), with the description of two new taxa from the Northern Andes. Zootaxa 3873:1–24.

Decker, K. L., A. M. Niklison, and T. E. Martin (2007). First description of the nest, eggs, and breeding behavior of the Merida Tapaculo. Wilson Journal of Ornithology 120:345–352.

Derryberry, E. P., S. Claramunt, G. Derryberry, R. T. Chesser, J. Cracraft, A. Aleixo, J. Pérez-Emán, J. J. V. Remsen, and R. T. Brumfield (2011). Lineage diversification and morphological evolution in a large-scale continental radiation: The Neotropical ovenbirds and woodcreepers (Aves: Furnariidae). Evolution 65:2973–2986.

Donegan, T. M., and J. E. Avendaño (2008). Notes on tapaculos (Passeriformes: Rhinocryptidae) of the Eastern Andes of Colombia and the Venezuelan Andes, with a new subspecies of *Scytalopus griseicollis* from Colombia. Ornitología Colombiana 6:24–65.

Fjeldså, J., M. D. Álvarez, J. M. Lazcano, and B. León (2005). Illicit crops and armed conflict as constraints on biodiversity conservation in the Andes region. AmBio 34:205–211.

Fjeldså, J., and N. Krabbe (1990). Birds of the High Andes. Zoological Museum, University of Copenhagen and Apollo Books, Svendborg, Denmark.

Freeman, B. G., and H. F. Greeney (2008). Parental care of the Long-tailed Tapaculo (*Scytalopus micropterus*) in northeastern Ecuador. Ornitologia Neotropical 19:581–585.

Ginés, H., R. Aveledo, A. R. Pons, G. Yépez, and R. Muñoz Tebar (1953). Lista y comentario de las aves colectadas en la región. In La Región de Perijá y sus Habitantes (Sociedad de Ciencias Naturales La Salle, Editor). Editorial Sucre, Caracas, Venezuela. pp. 225–277.

Ginés, H., and G. Yépez (1953). Ojeada general sobre la avifauna de la región. In La Región de Perijá y sus Habitantes (Sociedad de Ciencias Naturales La Salle, Editor). Editorial Sucre, Caracas, Venezuela. pp. 215–220.

Greeney, H. F. (2008). Additions to our understanding of *Scytalopus* tapaculo reproductive biology. Ornitología Neotropical 19:463–466.

Greeney, H. F., A. D. Bücker, and N. Harbers (2005). Parental care of the Blackish Tapaculo (*Scytalopus latrans*) in northeastern Ecuador. Ornitología Neotropical 16:283–286.

Greeney, H. F., and R. A. Gelis (2005). The nest and nestlings of the Long-tailed Tapaculo (*Scytalopus micropterus*) in Ecuador. Ornitología Colombiana 3:88–91.

Greeney, H. F., and C. J. F. Rombough (2005). First nest of the Chusquea Tapaculo (*Scytalopus parkeri*) in southern Ecuador. Ornitología Neotropical 16:439–440.

Hernández-Camacho, J., A. Hurtado-Guerra, R. Ortiz-Quijano, and T. Walschburger (1992). Centros de endemismo en Colombia. In La Diversidad Biológica de Iberoamérica Vol. I (G. Halffter, Editor). Acta Zoológica Mexicana (Volumen Especial). Xalapa, Mexico. pp. 175–190.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis (2005). Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25: 1965–1978.

Hilty, S. L. (2003). Birds of Venezuela. Princeton University Press, Princeton, NJ.

Hosner, P. A., and N. E. Huanca (2008). Nest, eggs and parental care of the Puna Tapaculo (*Scytalopus simonsi*). Wilson Journal of Ornithology 120:473–477.

Huelsenbeck, J., and F. Ronquist (2001). MrBayes: Bayesian inference of phylogenetic trees. Bioinformatics 17:754–755.

International Union for Conservation of Nature (IUCN) (2001). IUCN Red List Categories and Criteria: v3.1. IUCN species survival commission. http://www.iucnredlist.org/

Krabbe, N. (2008). Birds of the Sierra Nevada de Santa Marta, Colombia. J. V. Moore Nature Recordings, San Jose, CA.

Krabbe, N., and C. D. Cadena (2010). A taxonomic revision of the Paramo Tapaculo *Scytalopus* canus Chapman (Aves: Rhinocryptidae), with description of a new subspecies from Ecuador and Peru. Zootaxa 2354:56–66.

Krabbe, N., and T. S. Schulenberg (1997). Species limits and natural history of *Scytalopus* tapaculos (Rhinocryptidae), with descriptions of the Ecuadorian taxa, including three new species. In Studies in Neotropical Ornithology Honoring Ted Parker (J. V. Remsen, Editor). Ornithological Monographs, no. 48. pp. 47–88.

Krabbe, N., and T. S. Schulenberg (2003). Family Rhinocryptidae (tapaculos). In Handbook of the Birds of the World, Broadbills to Tapaculos, vol. 8 (J.del Hoyo, A. Elliott, and D. A. Christie, Editors). Lynx Edicions, Barcelona, Spain. pp. 748–787.

Lentino, M., C. Sharpe, J. L. Pérez-Emán, and Y. Carreño (2004). Aves registradas en la Serranía de Lajas, Serranía de Valledupar, Sierra de Perijá, Estado Zulia, en Abril del 2004. Technical report. Colección Ornitológica Phelps, Caracas, Venezuela.

López-O., J. P., J. E. Avendaño, N. Gutiérrez-Pinto, and A. M. Cuervo (2014). The birds of Serranía de Perijá: The northernmost avifauna of the Andes. Ornitología Colombiana 14:62–93.

Mata, H., C. S. Fontana, G. N. Maurício, M. R. Bornschein, M. F. de Vasconcelos, and S. L. Bonatto (2009). Molecular phylogeny and biogeography of the eastern Tapaculos (Aves: Rhinocryptidae: *Scytalopus, Eleoscytalopus*): Cryptic diversification in Brazilian Atlantic Forest. Molecular Phylogenetics and Evolution 53:450–462.

Maurício, G. N., R. Belmonte-Lopes, J. F. Pacheco, L. F. Silveira, B. M. Whitney, and M. R. Bornschein (2014). Taxonomy of "Mouse-colored Tapaculos" (II): An endangered new species from the montane Atlantic Forest of southern Bahia, Brazil (Passeriformes: Rhinocryptidae: *Scytalopus*). The Auk: Ornithological Advances 131:643–659.

Maurício, G. N., H. Mata, M. R. Bornschein, C. D. Cadena, H. Alvarenga, and S. L. Bonatto (2008). Hidden genetic diversity in Neotropical birds: Molecular and anatomical data support a new genus for the "*Scytalopus*" *indigoticus* species-group (Aves: Rhinocryptidae). Molecular Phylogenetics and Evolution 49:125–135.

Meyer de Schauensee, R. (1959). Additions to the "Birds of the Republic of Colombia." Proceedings of the Academy of Natural Sciences of Philadelphia 111:53–75.

Meyer de Schauensee, R. (1964). The Birds of Colombia and Adjacent Areas of South and Central America. Livingston Publishing Company, Narberth, PA.

Nylander JAA (2004). MrModeltest, version 2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University,Uppsala, Sweden.

Peters, J. L. (1951). Check-list of Birds of the World. Vol. 7. Museum of Comparative Zoology, Cambridge, MA, USA.

Phelps, W. H. (1943). Las Aves de Perijá. Boletín Sociedad Venezolana de Ciencias Naturales 8:265–338.

Phelps, W. H., and W. H. Phelps, Jr. (1950). Lista de las aves de Venezuela con su distribución, Tomo 2, Parte 2. Passeriformes. Boletín Sociedad Venezolana de Ciencias Naturales 12:1–427.

Phelps, W. H., and W. H. Phelps, Jr. (1953). Eight new subspecies of birds from the Perija mountains, Venezuela. Proceedings of the Biological Society of Washington 66:1–12.

Phelps, W. H., and W. H. Phelps, Jr. (1963). Lista de las aves de Venezuela con su distribución, Tomo 1, Parte 2. Passeriformes. Second edition. Boletín Sociedad Venezolana de Ciencias Naturales 24:1–479.

Phillips, S. J., R. P. Anderson, and R. E. Schapire (2006). Maximum entropy modelling of species geographic distributions. Ecological Modelling 190:231–259.

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

Rangel-Ch., J. O. (2007). La alta montaña de Perijá: consideraciones finales. In Colombia Diversidad Biótica V: La Alta Montaña de la Serranía de Perijá (J. O. Rangel-Ch, Editor). Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia. pp. 417–436.

Rangel-Ch., J. O., and H. Arellano-P. (2007). Vegetación de la alta montaña de Perijá. In Colombia Diversidad Biótica V: La Alta Montaña de la Serranía de Perijá (J. O. Rangel-Ch., Editor). Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia. pp. 173–192.

Remsen, J. V., Jr., C. D. Cadena, A. Jaramillo, M. Nores, J. F. Pacheco, J. Pérez-Emán, M. B. Robbins, F. G. Stiles, D. F. Stotz, and K. J. Zimmer (2014). A classification of the bird species of South America. [Version 29 September 2014]. American Ornithologists' Union. http://www.museum.lsu.edu/~Remsen/SACCBaseline.html

Ridgely, R. S., and G. Tudor (1994). The Birds of South America, vol. 2: The Suboscine Passerines. University of Texas Press, Austin, TX.

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

Rivera-Díaz, O., and J. L. Fernández-Alonso (2003). Análisis corológico de la flora endémica de la Serranía de Perijá, Colombia. Anales del Jardín Botánico de Madrid 60:347–369.

Simon, J. E., and S. Pacheco (2005). On the standardization of nest descriptions of neotropical birds. Revista Brasileira De Ornitologia 13:143–154.

Skutch, A. F. (1972). Studies of tropical American birds. Publications of the Nuttall Ornithological Club, No.10, Cambridge, MA.

Smith, C., and G. Londoño (2014). First description of nest, eggs, incubation behavior, and nestlings of Trilling Tapaculo (*Scytalopus parvirostris*). Wilson Journal of Ornithology 126: 81–85.

Smithe, F. B. (1975). Naturalist's Color Guide. American Museum of Natural History, New York, NY.

Smithe, F. B. (1981). Naturalist's Color Guide, Part III. American Museum of Natural History, New York, NY.

Stamatakis, A. (2006). RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22:2688–2690.

Strewe, R. (2004). Notas sobre una colonia de anidación del Vencejo pierniblanco (*Aeronautes montivagus*) en la Serranía de Perijá. Boletín SAO 14:2–4.

Valderrama, E., J. L. Pérez-Emán, R. T. Brumfield, A. M. Cuervo, and C. D. Cadena (2014). The influence of the complex topography and dynamic history of the Andes on the evolutionary differentiation of a montane forest bird (*Premnoplex brunnescens*, Furnariidae). Journal of Biogeography 41:1533–1546.

Viloria, A. I., and R. Calchi La C. (1993). Una lista de los vertebrados vivientes de la Sierra de Perijá, Colombia y Venezuela. BioLlania 9:37–69.

Vuilleumier, F. (1970). Insular biogeography in continental regions. I. The northern Andes of South America. American Naturalist 104:373–388.

Young, B. E., and W. Zuchowski (2003). First description of the nest of the Silvery-fronted Tapaculo (*Scytalopus argentifrons*). Wilson Bulletin 115:91–93.

Zimmer, J. T. (1939). Studies in Peruvian birds, no. 32. The genus *Scytalopus*. American Museum Novitates 1044:1–18.

APPENDIX A

Specimens of various taxa in the genus *Scytalopus* examined at the Colección Ornitológica Phelps (COP), Colección Adolfo Pons (PONS), Colección de Aves del Instituto Alexander von Humboldt (IAvH-A), Instituto de Ciencias Naturales (ICN), the National Museum of Natural History, Smithsonian Institution (USNM), and Louisiana State University, Museum of Natural Science (LSUMZ). Adult and juvenile specimens are included. Specimens included in phylogenetic analysis are highlighted with an asterisk.

S. latebricola (all from Magdalena, Colombia). Males (17): IAvH-A 2049, ICN 36194, 36257*, USNM 170554, 387414-5, 387417, 387420, 387422-25, 387429-31, 387433, LSUMZ 90420; females (14): ICN 23338, USNM 170553, 387412-4, 387416, 387418-19, 387421, 387426-8, 387432, 387434.

***S. perijanus* sp nov.** Males (25, not including the type series): USNM 369262-3, 369265, 369267, 373421, 373423, 373425, 373430, 373431-2, 373437, 373438 (La Guajira, Colombia), COP 54931, 54938-40, 54945, 72846-7, 72851-2, 72854, 74172, PONS 2890-1 (Zulia, Venezuela); females (20): USNM 369261, 369264, 369266, 369268, 373420, 373422, 373424, 373426-7, 373429, 373433-36 (La Guajira, Colombia), COP 54933, 54947, 57708, PONS 2889, 2892-3 (Zulia, Venezuela); unsexed (3): ICN 36045, 36046 (Cesar, Colombia), USNM 373428 (La Guajira, Colombia).

S. meridanus. Males (16): all from Venezuela: COP 14363, 14577, 45379, 45382, 49294-5, 73947 (Mérida), 9441, 11102, 24551, 83654-5, 84104, 84105*, 84108*, 84109 (Táchira); females (4): all from Venezuela: COP 14205, 65397, 71525 (Mérida), 84107* (Táchira); unsexed (2): COP 84106, 84110 (Táchira).

S. caracae. Males (17): all from Venezuela: COP 13051, 13153, 13155, 56785, 58461, 58466, 58468, 58471-72, 61643, 61645, 62230, 62610, 62612-3, 62619, LSUMZ 14194 (Caracas D.F.); females (10) all from Venezuela: COP 13049-50, 56782, 58464, 61648, 62606, 62609, 62616, 62618 (Caracas D.C.), 75775 (Aragua).

S. griseicollis. Males (19) all from northeastern Colombia: IAvH-A 8416, 14919*, 14841, 14946, 14797, 14948, 12068, 12125*, 10728, 10664, USNM 373414 (Norte de Santander), ICN 36121, 36416, 37514, 37538, 37548, 37570, USNM 402075, 411789 (Santander); females (12) all from Colombia: IAvH-A 8427, 8434, 8438, 10625, 12123, 14941, USNM 373415 (Norte de Santander), ICN 37516, 37522, USNM 313714, 402074, 411790 (Santander).

APPENDIX B

Recordings of primary songs and calls of *Scytalopus perijanus* sp. nov., *S. latebricola*, *S. meridanus*, and northern *S. griseicollis* used in quantitative analyses of vocalizations. We used the average of 2 to 4 song bouts per individual for *S. perijanus* and northern *S. griseicollis*, and the values from one song per individual for *S. latebricola* and *S. meridanus*. Two calls per individual were analyzed for *S. perijanus*, whereas 1 to 2 calls per individual were considered for the other species. Alternative and advertising songs of *S. perijanus* are also listed below. Acronyms for sound archives: CSA, Colección de Sonidos Animales-Instituto Alexander von Humboldt, XC, xeno-canto.

Primary Songs

S. perijanus: Colombia, Cesar, Manaure, Sabana Rubia (J. E. Avendaño, CSA 2801-2; J. P. López, CSA 2803; A. M. Cuervo, CSA 2804-5); Colombia, Cesar, Manaure, San Antonio (A. M. Cuervo, CSA 2806-8). ***S. latebricola***: Colombia, Magdalena, Santa Marta, San Lorenzo ridge (Krabbe 2008, # 1, 2, 4, 7; Strewe et al. 2005, # 27; C. Hesse, XC10186); ***S. meridanus***: Venezuela, Táchira, Páramo del Zumbador (Boesman 1999, # 2.1); Venezuela, Mérida, 10 km SE La Azulita (C. Parrish, XC6236; A. Spencer, XC14790); Venezuela, Mérida, Sierra Nevada N. P., Pico Humboldt trail (D. Edwards, XC20071); Venezuela, Mérida, Sierra Nevada N. P., La Mucuy (J. Klaiber, XC43158, XC43160); ***S. griseicollis*** (northern): Venezuela, Apure, Rio Oirá (C. Parrish, XC16656); Colombia, Santander, California, Angosturas (J. E. Avendaño, XC86713-15).

Calls

S. perijanus: Colombia, Manaure, above El Cinco (A. M. Cuervo, CSA 2809; J. E. Avendaño 2810); Colombia, Manaure, Sabana Rubia, Casa de Vidrio (J. E. Avendaño, CSA 2811-13; A. M. Cuervo, CSA 2814-15); Colombia, Manaure, San Antonio (A. M. Cuervo, CSA 2816); ***S. latebricola***: Colombia, Magdalena, Santa Marta, San Lorenzo ridge (Krabbe 2008, # 9, 11; C. Hesse, XC10187; N. Athanas, XC10746; D. Geale, XC51259); Colombia, Cesar, 3–8 km NNW Nabusimake (Krabbe 2008, # 10, 19);

S. meridanus: Venezuela, Táchira, Páramo de Batallón (Boesman 1999, # 2.4); Venezuela, Mérida, Sierra Nevada N. P., Loma Redonda-La Aguada (B. López-L, XC50485-86); Venezuela, Mérida, Sierra Nevada N. P., La Mucuy (B. López-L, XC50641); ***S. griseicollis*** (northern): Venezuela, Apure, Rio Oirá (C. Parrish, XC6079, XC16657, XC16659, XC16661); Venezuela, Táchira, Betania, Tamá N. P. (A. Renaudier, XC23330-32); Colombia, Santander, Guasca, vereda Concepción (O. Cortés, XC27187); Colombia, Santander, Suratá, vereda Bucaré (J. E. Avendaño, XC86716-17).

Alternative songs.—***S. perijanus***: Colombia, Manaure, Sabana Rubia, Casa de Vidrio (J. E. Avendaño, CSA 2817-18; A. M. Cuervo, CSA 21819); Colombia, Manaure, El Cinco, above El Cinco (A. M. Cuervo, CSA 2820-21).

Advertising song

S. perijanus: Colombia, Manaure, above El Cinco (J. E. Avendaño, CSA 2822).

APPENDIX C

List of localities of *Scytalopus perijanus* sp. nov. (geographical coordinates in decimal degrees and elevation above sea level) used in ecological niche-modeling analysis (Figure 8). Locality data were obtained from museum specimens, song recordings and reliable observations. Colombia, La Guajira: Sierra Negra, Monte Elías (10.832, –72.686), 1,530-1,830 m; Tierra Nueva (10.614, –72.801), 1,370–1,830 m. La África (10.524, –72.935), 1,615 m. Cerro Pintado, Laguna de Junco (10.445, –72.902), 2,290–2,740 m; Cerro Pintado (10.5, –72.887), 3,230 m; Cesar: Municipality of Manaure, Sabana Rubia, Casa de Vidrio (10.367, –72.897), 3,030 m; El Cinco, above El Cinco (10.364, –72.953), 2,450 m; San Antonio, Finca Villaluz (10.364, –72.993), 1,600–1,800 m. Camp above Hiroca, S Cerro La Teta (9.93, –73.046), 1,675–1,980 m. Cesar: Municipality of La Paz, corregimiento de San José de Oriente, Brisas del Perijá (10.262, –72.962), 2,800–3,000m. Venezuela, Zulia: Cerro Viruela, NW foot Cerro Pintado (10.457, –72.884), 3,180–3,230 m; Campamento Frontera 5, foot Cerro Pintado (10.439, –72.862), 2,710 m. Serranía de Las Lajas, Antenas (10.437, –72.738), 1,800-1,850 m. Campamento Avispa, Fila Macoita y Apón (10.403, –72.837), ~2,000 m. Pie Nudo 4 (10.394, –72.792), ~1,900 m. Cerro Tamuypejocha or Pejochaina, Cumbre y falda (10.095, –72.815), 2,300 m. Río Negro, Manchique abajo (10.071, –72.847). Cerro Tetare or La Teta, Pie SE (10.036, –72.935), ~2,900 m. Campamento Frontera 2 (10.029, –72.878), 2,270 m.