

## A taxonomic revision of the Paramo Tapaculo *Scytalopus canus* Chapman (Aves: Rhinocryptidae), with description of a new subspecies from Ecuador and Peru

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### Abstract

The nominate subspecies of the Paramo Tapaculo (*Scytalopus canus* Chapman), which is restricted to high elevations of the Western Andes of Colombia, differs substantially in song from *S. c. opacus* from the Central Andes of Colombia, Ecuador, and northern Peru. In accordance with current taxonomy of the genus, which is primarily based on differences in song, we assign species rank to both taxa. Within *opacus*, birds from southernmost Ecuador and northernmost Peru sing like northern *opacus* but call differently. They are indistinguishable morphologically except for a white patch in the wing present in 10 out of 12 of the adult males of the southern population. We describe this population as a new taxon and rank it as a subspecies of *S. opacus*. Genetically, *S. canus*, nominate *S. opacus*, and the new taxon are strongly differentiated (>5% divergence in mtDNA); the first two appear to be sister taxa.

**Key words:** *Scytalopus*, tapaculo, Andes, Colombia, species limits, subspecies

### Resumen

[Una revisión taxonómica del Tapaculo de Páramo *Scytalopus canus* (Aves: Rhinocryptidae), con una descripción de una nueva subespecie de Ecuador y Perú]

La taxonomía a nivel de especies de muchos tapaculos del género *Scytalopus* (Aves: Rhinocryptidae) no ha sido aclarada. La subespecie nominal del Tapaculo de Páramo (*Scytalopus canus* Chapman), que se encuentra restringida a las elevaciones altas de la Cordillera Occidental de los Andes de Colombia, difiere sustancialmente en el canto en comparación con *S. c. opacus* de la Cordillera Central de Colombia, Ecuador y el norte de Perú. De acuerdo con la taxonomía actual del género, la cual se basa principalmente en diferencias en el canto, le asignamos el rango de especie a ambos taxones. Las aves del extremo sur de Ecuador y el extremo norte de Perú cantan como *opacus* pero tienen reclamos diferentes. Éstas son indistinguibles de *opacus* en su morfología, excepto porque 10 de 12 machos adultos presentan un parche blanco en cada ala. Describimos esta población como un nuevo taxón, que tratamos como una subespecie de *S. opacus* debido a la similitud de sus cantos y morfología. Sin embargo, análisis adicionales podrían indicar que merecen tratarse como especies diferentes. Genéticamente, *S. canus*, la forma nominal de *S. opacus* y el taxón nuevo están marcadamente diferenciados (>5% de divergencia en ADN mitocondrial); las primeras dos formas parecen ser hermanas.

**Palabras clave:** Andes, Colombia, límites de especies, subspecies

### Introduction

*Scytalopus* tapaculos constitute one of the greatest challenges to avian taxonomy. Many species look so similar that some specimens cannot be identified with certainty. Voice is believed to be the primary means of

communication, and individuals with similar vocalizations have been found to be genetically similar (Arctander & Fjelds  1994). Accordingly, vocal characters have been instrumental in defining species limits in the genus, and in recent years the number of recognized species has risen from ten to nearly forty (Krabbe & Schulenberg 1997; Remsen *et al.* 2009). The Paramo Tapaculo (*Scytalopus canus* Chapman) is common in treeline scrub in the Northern Andes of Colombia, Ecuador, and northern Peru. It was described by Chapman (1915) on the basis of ten specimens collected at an elevation of 12500 feet (3810 m) in the P ramo de Paramillo, northwestern Antioquia Department, Western Andes of Colombia. Nearby P ramo de Frontino was later added to its known range by Hilty & Brown (1986), who mentioned two immatures collected there. Cory & Hellmayr (1924) referred a specimen collected at La Leonera, Central Andes, Caldas Department, to *canus*, but Krabbe & Schulenberg (1997) treated this allocation with some doubt. Zimmer (1939) described two specimens from Tambillo on the upper R o Upano in Morona-Santiago Province, Ecuador, as a new taxon (*obscurus*, now known as *opacus*; Zimmer 1941), diagnosed from *canus* by its longer wings and tail and by a small amount of brownish color with dark bars on the posterior underparts; these parts are uniform gray in *canus*. Zimmer considered *canus* and *opacus* each other's closest relatives, but ranked them as subspecies of a broad *S. magellanicus* (Gmelin).

Krabbe & Schulenberg (1997) afforded species rank to all vocally known taxa in Zimmer's *S. magellanicus*. They showed that all, including *opacus*, have distinctive songs, but were unable to assess the taxonomic status of *canus* because it was vocally unknown. Therefore, they left *opacus*, its presumed closest relative, as a subspecies of *canus*. They referred to *S. c. opacus* two distinct populations, one north, the other south of the R o Zamora, with similar songs but drastically different calls.

We here provide evidence that although *canus* and *opacus* are indeed each other's closest relatives, the two have distinct songs that are as different as or more different than those of other species in the genus and are highly differentiated genetically, suggesting they should be considered different species, with *canus* genuinely restricted to the Western Andes of Colombia. We also name the southern population of *opacus* as a new taxon, which we conservatively treat as a subspecies because it and the northern population have similar songs.

## Methods

On 6–12 August 2004, NK made tape recordings of ca.15 individuals of nominate *S. canus* at the treeline on P ramo de Frontino at elevations ranging from 3300–3500 m (see details on study site in Krabbe *et al.* 2005). A single adult male was collected; the skin specimen was deposited in the Instituto de Ciencias Naturales, Universidad Nacional de Colombia (ICN 35020) and a tissue sample in the collection of Instituto Alexander von Humboldt (IAvH-CT 5178). The recordings were compared to recordings of the two populations of *opacus* (Table 1), all publicly accessible at [www.xeno-canto.org](http://www.xeno-canto.org), Macaulay Library of Natural Sounds, Cornell University, or in Banco de Sonidos Animales, Instituto Alexander von Humboldt, Colombia. Specimens of *opacus* in the Zoological Museum, University of Copenhagen (ZMUC) and data on other museum specimens obtained previously (Krabbe & Schulenberg 1997) were reexamined. Measurements and notes on plumage of the specimen from Depto. Caldas in the Central Andes were obtained. Plumage descriptions of four additional specimens in the Museum of Natural Science, Louisiana State University (LSUMZ) of southern *opacus* from Zamora-Chinchipe, Ecuador (83373, adult male) and Cajamarca, Peru (169860-62, immature male, adult female, juv male, respectively) were obtained.

**TABLE 1.** Number of tape-recordings of different individuals examined.

Taxon	Song	Calls
<i>S. canus canus</i>	14	10
<i>S. canus opacus</i> northern	27	33
<i>S. canus opacus</i> southern	11	10

CDC examined phylogenetic relationships and patterns of genetic variation within the *S. canus* complex using DNA sequences of the mitochondrial gene ND2 (c. 1000 base pairs) obtained following methods described in a recent study (Maurício *et al.* 2008). Analyses were based on sequence data from that study (including sequences of the specimen of *S. c. canus* collected by NK at Páramo de Frontino and of *Scytalopus vicinior*, *S. stilesi*, *S. pachecoi*, *S. magellanicus*, and as outgroup, *Eugralla paradoxa*), supplemented with new data obtained for three specimens of *S. canus opacus*. These include one specimen from 100 km north of the Río Zamora (ZMUC 125150, from Zapote Najda Mts., Morona-Santiago, Ecuador, 3°01'S, 78°39'W, 3450 m), one from 100 km south of the Río Zamora (ZMUC 125688, from the upper Río Isimanchi, Zamora-Chinchiipe, Ecuador 4°45'S, 79°25'W, 3150 m), and one from 100 km further south, in northern Peru (LSUMZ B31950, from Quebrada Lanchal above Sallique, Cajamarca, 5°41'S, 79°15'W, 2900 m; see acknowledgements for museum acronyms). In addition, our data set included new sequences for two specimens representing species that belong in lineages that are closely related to the *canus* (*sensu lato*) group according to preliminary analyses that considered nearly all species in the genus (C.D. Cadena *et al.*, unpubl. data): *S. affinis* Zimmer (ZMUC 125154) and *S. superciliaris* Cabanis (MBM 8242). New sequences were deposited in GenBank (accession numbers GU325813-GU325817).

Phylogenetic relationships among the selected taxa were reconstructed using maximum-likelihood, Bayesian inference, and maximum parsimony methods. The maximum-likelihood analysis was conducted using default settings in the program RAxML (Stamatakis 2006) run on the CIPRES Portal (<http://www.phylo.org>); nodal support was estimated using 1000 bootstrap replicates (Stamatakis *et al.* 2008). The program BEAST (Drummond & Rambaut 2007) was employed for Bayesian inference using the HKY+G model (selected as the best fit to the data based on the Akaike Information Criterion in Modeltest; Posada & Crandall 1998) and an uncorrelated relaxed lognormal clock model with a Yule process tree prior; the analysis was run twice independently for  $5 \times 10^7$  generations, of which the first  $1 \times 10^7$  were discarded as burn-in in each case. Results from both runs were entirely consistent and both resulted in large effective sample sizes for parameters, suggesting they adequately sampled the posterior distributions. As a complement to these model-based analyses, we performed a parsimony bootstrap analysis with 1000 replicates in the program PAUP\* (Swofford 2002).

## Results

The male taken at the Páramo de Frontino is the first adult specimen of *S. c. canus* collected away from the type locality, Páramo de Paramillo. These two localities are separated by c. 70 km with no pass lower than 2150 m elevation between them (passes 300 m lower within the range of northern *opacus* have not caused discernible differentiation in that form). Additionally, the specimen shows no trace of dark barring or brown in the flanks, and its wings and tail measure 52 and 35 mm, respectively (Table 2). Thus, it agrees with the description of the type series of *canus* (Chapman 1915, additional measurements given by Cory & Hellmayr 1924), leaving little doubt that it represents this taxon. Its body mass was 14.5 g, the first recorded for nominate *S. canus*. The male specimen from La Leonera in the Central Andes (Carnegie Museum 70683) shows traces of barring on the upper tail coverts, flanks and thighs, and has a wing of 54.5 mm and a tail of 40.2 mm (Table 2). This suggests that it belongs with *opacus*, as suspected by Krabbe & Schulenberg (1997), an allocation further established by song and call notes tape-recorded nearby in the Central Andes (see below). Thus, *canus* appears to be restricted to the Western Andes.

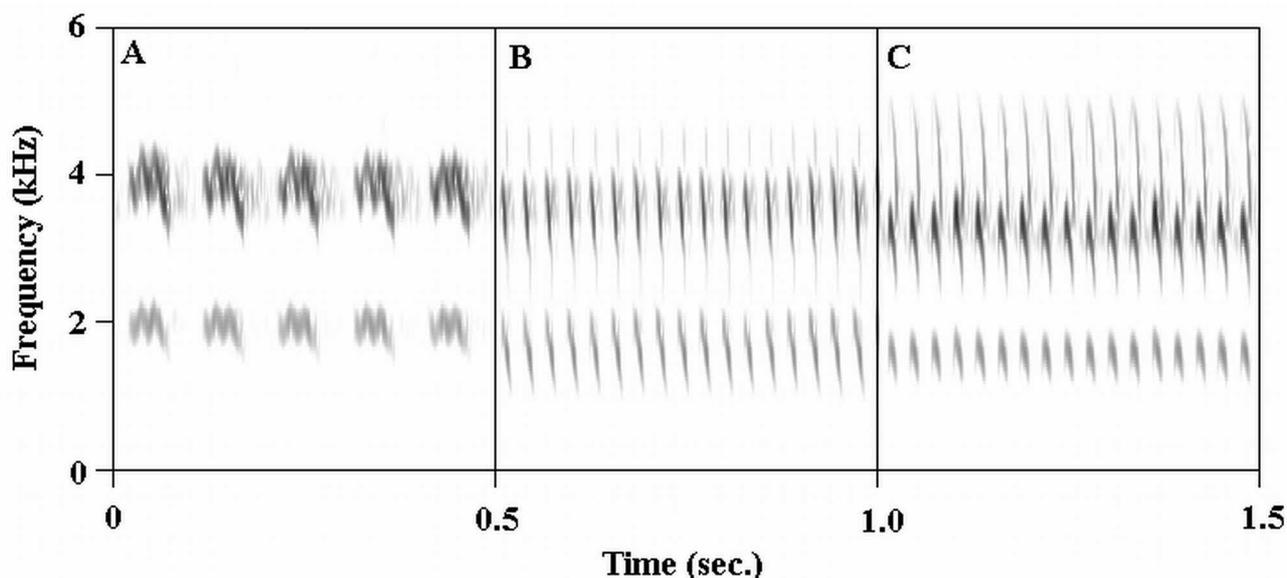
The song of *canus* is of about the same duration as the song of *opacus* (4–12 s) but differs in five aspects (Table 3; Figs. 1–2): 1) it is much slower paced, 7–11 instead of 30–40 notes per s (Fig. 1); 2) the notes are churring rather than simple down- or up-down-strokes (Fig. 1); 3) the pace changes through the song, accelerating 14–43% instead of being constant or more commonly decelerating 4–27%; 4) the pitch falls by three to seven half notes on a diatonic scale, most drastically during the beginning of the song, instead of being constant or falling more gradually and at the most by two half notes (Fig. 2); 5) the pitch is higher, 3.5–5.6 instead of 3.1–4.1 kHz (Figs. 1–2). Both song and call notes of birds from the northern part of the Central Andes of Colombia are similar to those of *S. c. opacus*.

**TABLE 2.** Wing and tail measurements for *S. c. canus*, populations of *S. c. opacus* from north and south of Río Zamora, and two specimens from Páramo de Frontino, Antioquia (ICN 35020) and La Leonera, Caldas (CM 70683). Measurements of the Antioquia specimen agree with *S. c. canus*, those of the Caldas specimen with *S. c. opacus*. Measurements given of nominate *S. canus* are from the type series, those of *S. c. opacus* from Krabbe & Schulenberg (1997).

Taxon	Sex	Wing flat (mm): mean (range) n	Tail (mm): mean (range) n
<i>S. c. canus</i>	M	52.5 (50–55) n=2	35 n=2
<i>S. c. canus</i> (ICN 35020)	M	52	35
<i>S. c. opacus</i> (CM 70683)	M	54.5	40.2
<i>S. c. opacus</i> (northern)	M	57.2 (52–63) n=22	42.8 (35.4–46.7) n=19
<i>S. c. opacus</i> (southern)	M	57.8 (55–59) n=8	43.4 (39–47) n=8
<i>S. c. canus</i>	F	52.6 (52–53) n=3	33.8 (32–35) n=3
<i>S. c. opacus</i> (northern)	F	55.3 (54–56) n=4	39.8 (39–42) n=4
<i>S. c. opacus</i> (southern)	F	55.5 (55–56) n=2	40.4 (39–41.7) n=2

**TABLE 3.** Some properties of songs of *Scytalopus c. canus* and northern and southern populations of *S. c. opacus*. Positive values for  $\Delta$  Pace are indicated with the prefix 'acc' (accelerating), negative values with 'dec' (decelerating). The pitch given is that of the second harmonic.  $\Delta$  Pitch is negative for all three and is measured in half notes on the diatonic scale.

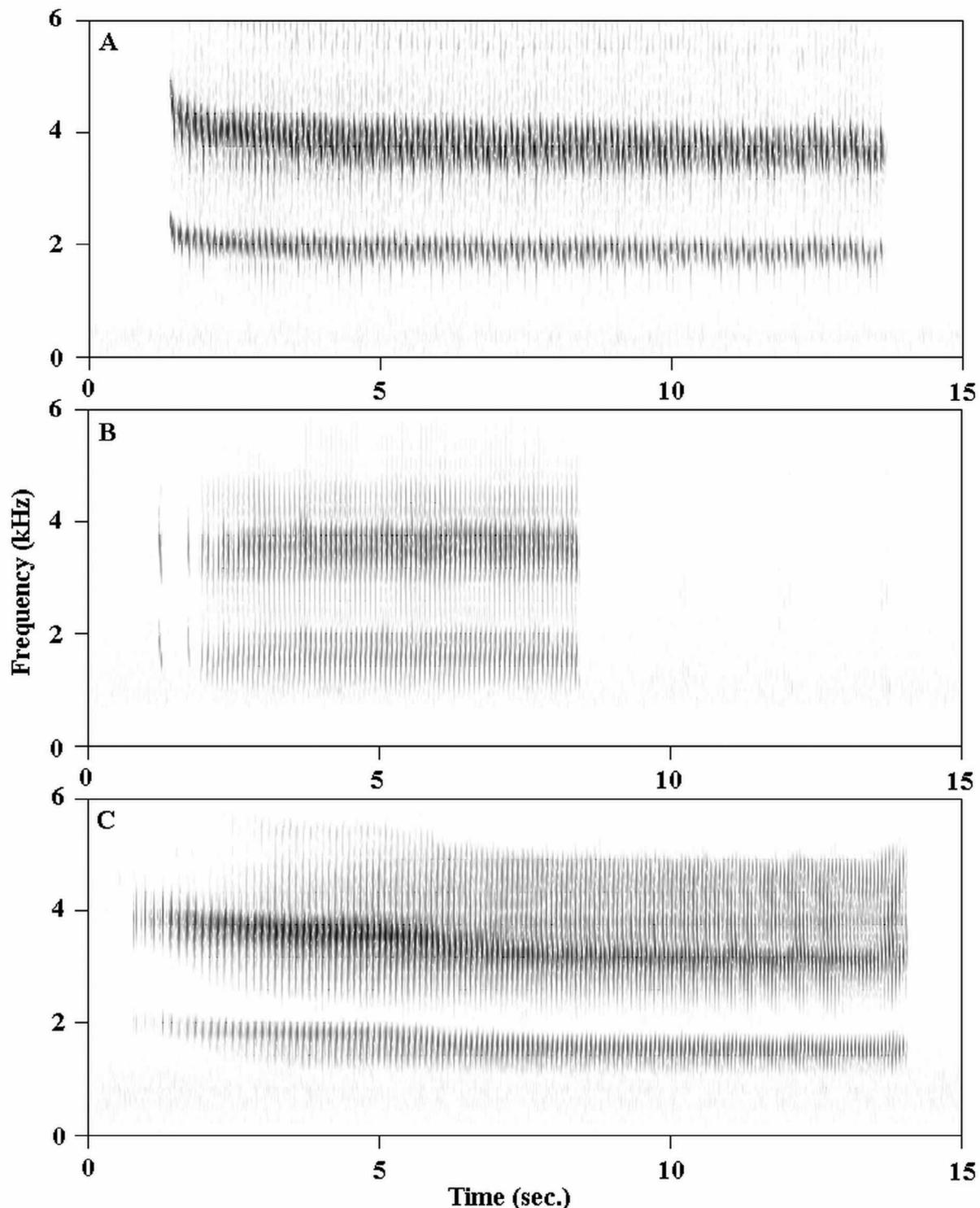
Taxon	N	Duration (s)	Pace (notes/s)	$\Delta$ Pace (%) mean and range	Pitch (kHz)	$\Delta$ Pitch (half notes)
<i>S. c. canus</i>	9	4–12	7–11	acc 27 (14–43)	3.5–5.5	3–7
<i>S. c. opacus</i> northern	21	4–12	29–40	dec 7 (0–11)	3.2–4.0	0 (-2)
<i>S. c. opacus</i> southern	9	4–12 (-120)	29–43	dec 16 (4–27)	3.1–4.1	0 (-2)



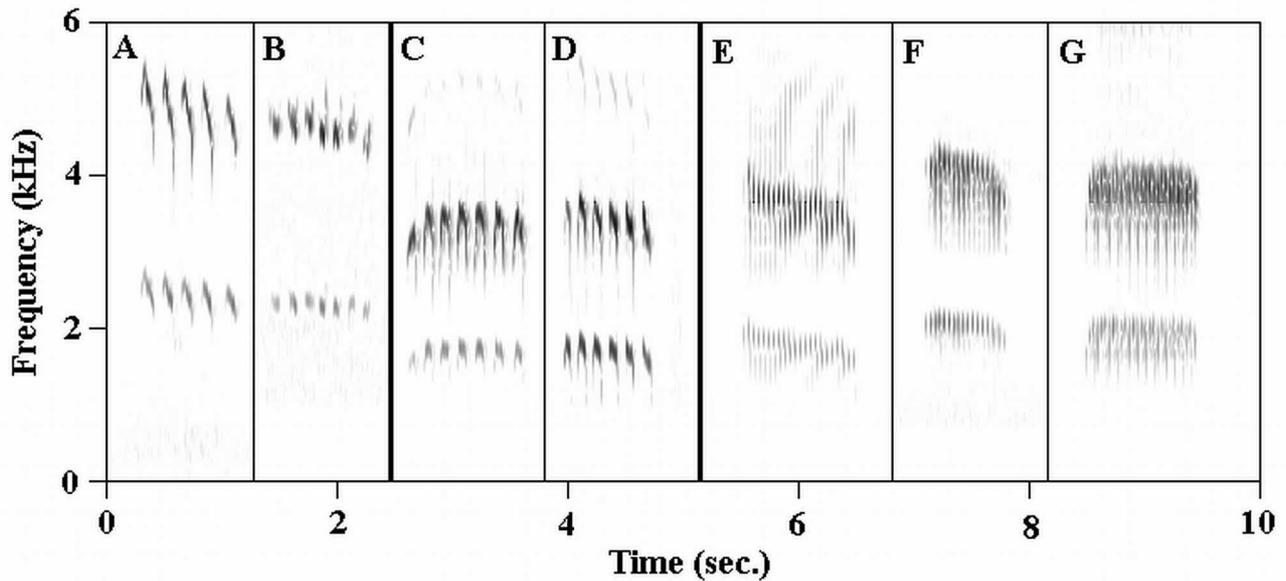
**FIGURE 1.** Half second sequences of songs of (A) *Scytalopus c. canus* from Frontino, Antioquia, Colombia, (B) northern *S. c. opacus* from Azuay, Ecuador, and (C) southern *S. c. opacus* from Zamora-Chinchipe, Ecuador. Notice the churring, higher pitched and much slower paced notes of *S. c. canus*. Differences in note quality between northern and southern *S. c. opacus* are not constant.

The calls of *canus* are much like those of northern populations of *opacus* (Fig. 3). They resemble them in quality and pattern, but are higher pitched, 4.5–5.6 instead of 3.1–4.2 kHz. They also tend to be composed of fewer notes, usually 3–5 instead of 5–8, that are given at a slower pace (4–6 instead of 5–10 per s). Calls of

birds from the Central Andes of Colombia (Huila, Quindío) are composed of 5–12 notes, paced 7–9 per s, and pitched 3.1–3.4 kHz, and are in all other aspects typical of *opacus*. The calls of birds from southern Ecuador and northernmost Peru, however, differ strikingly from calls of more northerly populations. They are like one second long reminiscences of song, with notes given at 19–27 per s at a slightly decreasing pace, with pitch constant or falling up to two half notes (Fig. 3).



**FIGURE 2.** Complete songs of (A) *Scytalopus c. canus* from Frontino, Antioquia, Colombia, (B) northern *S. c. opacus* from Azuay, Ecuador, and (C) southern *S. c. opacus* from Zamora-Chinchiipe, Ecuador. Notice that in *S. c. canus* the pitch falls rapidly in the beginning of the song. As in the example shown, most songs of northern *S. c. opacus* have one to three introductory notes. The song length of all three ranges from 4 to 12 s.



**FIGURE 3.** Calls of (A–B) *Scytalopus canus canus* from Frontino, Antioquia, Colombia, (C–D) northern *S. c. opacus* from Tungurahua and Carchi, Ecuador, and southern *S. c. opacus* from (E) Piura, Peru and (F–G) Zamora-Chinchipe, Ecuador.

Molecular data indicated the existence of three well-differentiated genetic lineages within the *S. canus* complex: *S. c. canus*, the northern form of *S. c. opacus* and the southern form of *S. c. opacus*. Pairwise mtDNA sequence divergence between members of these three forms exceeded 5%, whereas divergence between individuals of the southern form of *S. c. opacus* (the only one for which we had data for more than one individual) were negligible (Table 4). The three phylogenetic methods employed (maximum-likelihood, Bayesian inference, and maximum parsimony) indicated that *S. canus canus* is sister to the northern form of *S. c. opacus*, a relationship that received strong support in maximum-likelihood and maximum parsimony analyses (94% and 83% bootstrap), but was weakly supported in the Bayesian analysis (posterior probability 0.74 ; Fig. 4).

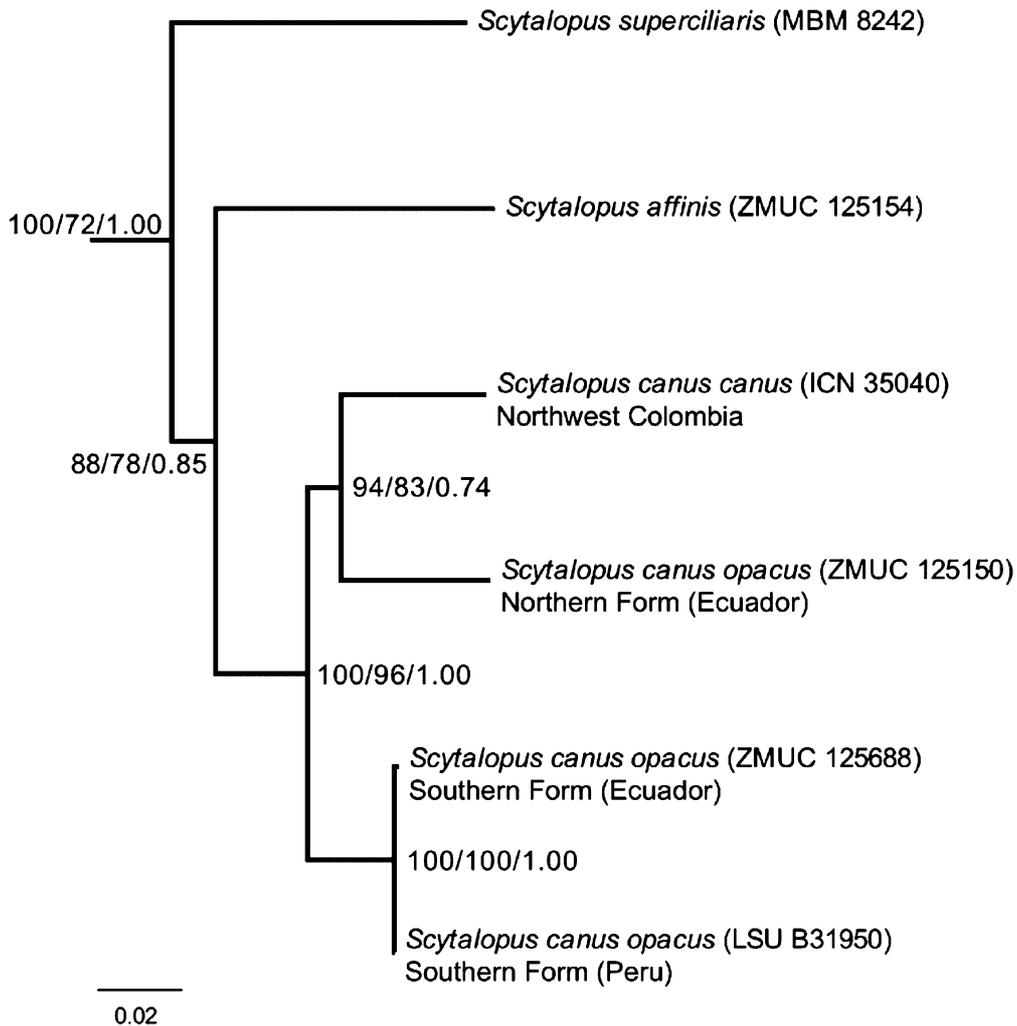
**TABLE 4.** Uncorrected sequence divergence (*p* distance) in the ND2 mitochondrial gene between specimens in the *Scytalopus canus* complex. Note the strong differentiation between nominate *S. canus* (1), the northern form of *S. c. opacus* (2), and the southern form of *S. c. opacus* (3–4).

Taxon	1	2	3
1. <i>S. canus canus</i> ICN 35020	-		
2. <i>S. canus opacus</i> ZMUC 125150	0.05604	-	
3. <i>S. canus opacus</i> ZMUC 125688	0.05320	0.05319	-
4. <i>S. canus opacus</i> LSUMZ B31950	0.05237	0.05242	0.00097

## Discussion

Our analyses reveal the existence of pronounced geographic variation in songs, calls, and mitochondrial DNA sequences within the *Scytalopus canus* complex. This variation is also matched by some degree of morphological variation. The differences in song between *canus* and *opacus* are as great as or greater than the differences between several other forms in Zimmer's broad *S. magellanicus*, which were elevated to biological species rank by Krabbe & Schulenberg (1997). Accordingly, we propose to rank these taxa as two separate biological species, Paramillo Tapaculo (*S. canus*) and Paramo Tapaculo (*S. opacus*). Being the better-

known species, we suggest retaining the English name Paramo Tapaculo for *S. opacus* and propose a new name for the heretofore virtually unknown *S. canus*.



**FIGURE 4.** Phylogram showing relationships among members of the *Scytalopus canus* complex and near relatives estimated based on maximum-likelihood (ML) analysis of sequences of the mitochondrial gene ND2. Values on the nodes indicate ML bootstrap support, MP bootstrap support, and Bayesian posterior probabilities.

Apart from their distinctive calls, populations of *S. opacus* from south of the Río Zamora can be distinguished from those north of this river by the white greater primary coverts (see illustration in Krabbe & Schulenberg 2003) present in 7 out of 9 adult males (and three more observed in the field). This includes specimens of males collected 50 km apart, but none of 5 female specimens. Thus, at least one distinctive plumage feature allows the recognition of southern populations as a separate taxon. Additionally, the southern population differs genetically from the northern populations by more than 5% sequence divergence in the ND2 gene. Despite these differences, which are sufficient grounds to consider both forms of *S. opacus* as different phylogenetic (Cracraft 1983) and evolutionary (Wiley 1978) species, these two populations do not differ appreciably in songs. Current species-level taxonomy of this group follows the biological species concept (sensu Johnson *et al.* 1999) and is based largely on differences in songs (Krabbe & Schulenberg 2003; Remsen *et al.* 2009).

Correspondence and geographic cohesiveness between distinctive song and genetic differentiation has been shown for a number of *Scytalopus* taxa (Arctander & Fjelds  1994; Cuervo *et al.* 2005; Bornschein *et al.* 2007; CDC *et al.* unpublished data). Likewise, some forms with similar songs but different calls, i.e., *S. pachecoi* Maur cio and *S. diamantinensis* Bornschein *et al.* (Bornschein *et al.* 2007) and southern and

northern populations of *S. opacus*, have been isolated genetically for extensive periods. Another case is that of populations of *S. spillmanni* Stresemann from the Western Andes of Colombia, which have fairly similar songs but distinctly different calls and were noted by Krabbe and coworkers (2006) to be genetically similar to birds from Ecuador, which actually differ by 2–3% sequence divergence from individuals from the Eastern Andes of Colombia and from Ecuador (CDC unpubl. data). However, because all these pairs of taxa are allopatric, ascribing their genetic divergence to reproductive isolation resulting from variation in calls is not possible. Although in at least one genus of suboscine birds (*Hypocnemis* antbirds) calls appear to play a crucial role in reproductive isolation (Isler *et al.* 2007), the importance of calls as mating barriers between *Scytalopus* species remains to be shown. Thus, unless future studies examining the function of songs and calls suggest otherwise, we conservatively apply species rank only to *Scytalopus* populations with distinctive songs, the approach employed by Krabbe & Schulenberg (1997, 2003). Therefore, despite the long genetic isolation of southern from northern populations of *S. opacus* and their distinct calls, the two have such similar songs and are morphologically so similar that we prefer to rank them as conspecific based on the available data.

Considering our phylogenetic analyses, treating the northern and southern populations of *S. opacus* *sensu stricto* as conspecific implies the recognition of a paraphyletic biological species, within which *S. canus* appears to be nested. Because the biological species concept emphasizes ability to interbreed and not common ancestry, and because paraphyletic biological species often result from differentiation of populations in the periphery of ranges (a likely biogeographic scenario for the differentiation of *S. canus*), the recognition of such entities is not at odds with the philosophy of this species concept (Donoghue 1985; Funk & Omland 2003). In addition, we note that paraphyly of *S. canus* is not strongly supported in all of our analyses, and recognize that phylogenetic patterns (but not degree of mtDNA differentiation) might change if one considers additional individuals or loci. In any event, we emphasize that conducting studies on the function of calls and songs in mate recognition in *Scytalopus* is an important priority in order to determine whether biological species rank for the southern population of *S. opacus* might be warranted. For the time being, however, we conservatively name this population as a new subspecies:

#### ***Scytalopus opacus androstictus* ssp. nov. Krabbe & Cadena**

**HOLOTYPE:** An adult male, deposited in the Zoological Museum, University of Copenhagen (ZMUC 80126). Collected by N. Krabbe (collector's number NK12-9.11.92) on 9 November 1992 along the Jimbura-Zumba road in Cordillera de Las Lagunillas, Loja Province, Ecuador (4°43'S, 79°26'W; 3450 m). Tissue sample in ZMUC (number 125728). A recording of the song of this individual was deposited on XenoCanto (number 35112).

**Diagnosis.** Similar in measurements and plumage coloration to *S. opacus opacus* from northern Ecuador and central Colombia, but differs vocally by its song-like call, and genetically. Additionally, in seven of nine adult males (and three more observed in the field) most or all of the greater primary coverts in both wings are albinistic, a trait not reported in nominate *S. opacus*.

**Description of holotype.** Capitalized color names and numbers from Smithe (1975): Above Blackish Neutral Gray (82), wings and tail very faintly washed with Brussels Brown (121B), rump and tips of tertials with faint, 1 mm wide bars of this color and blackish. Greater primary coverts white. Underparts including underwing uniform, between Dark Neutral Gray (83) and Medium Neutral Gray (84), tips of feathers of lower flanks and under tail coverts with 1 mm wide blackish and Tawny Olive (223D) bars. Weight 16.8 g. Wing chord 53 mm, wing flat 56 mm, tail length 39 mm, tarsus length 22.3 mm. Bill from fore edge of operculum 5.4 mm, from skull 10.3 mm, from mandible fork 6.4 mm. Tail composed of ten rectrices. Irides dark brown, maxilla blackish, mandible blackish brown, feet (tarsi and toes) fuscous. Testes medium enlarged (5 x 2.5 mm), seminal vesicle enlarged. Stomach contents: remains of small insects.

**Variation among males.** The nine adult males examined are remarkably uniform. Seven individuals vary slightly in the coloration of the primary coverts, which range from being mostly to entirely white; three

additional individuals observed in the field possessed this spot, but two adult male specimens from southernmost Zamora-Chinchi (ZMUC 80128, LSUMZ 83373) show no white and thus do not differ from nominate *S. opacus* morphologically.

**FEMALE:** Two adult and two subadult females appear indistinguishable from corresponding plumages of nominate *S. opacus*.

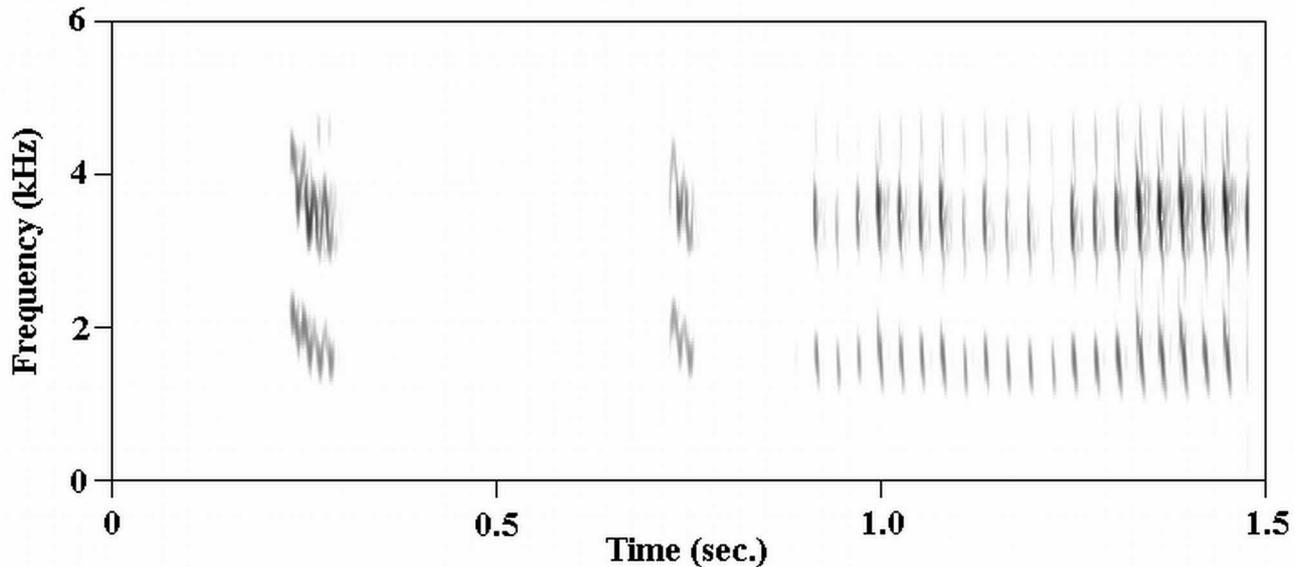
**Description of juvenile.** A recently fledged male (ZMUC 80131) with tail still in pin and crown feathers tipped with long down is Prout's Brown (121A) above, lightly barred blackish and with narrow buff tips on the secondaries. The throat and breast are Pale Pinkish Buff (121D) lightly mottled with blackish, belly dirty white and unbarred, sides, flanks and vent dirty white grading to Mikado Brown (121C) on sides of lower breast, and barred blackish. The upperparts are slightly darker brown and the belly paler than in four specimens of nominate *S. opacus*, but this difference might not be constant, considering the broad range of plumage variation seen in juveniles of nominate *S. o. opacus*, even within a locality (Krabbe & Schulenberg 1997).

**Distribution and habitat.** *S. o. androstictus* inhabits the East Andes south of the Río Zamora in southern Ecuador, and the Andes of northernmost Peru north of the Río Marañón, on the eastern flank of the Huancabamba valley. It occurs in treeline scrub at elevations ranging from 3000 to 3650 m, locally down to 2600 m along exposed ridges. On the eastern slopes it is replaced below and in taller and more bamboo-dominated vegetation by *S. parkeri* Krabbe & Schulenberg and also meets the (as yet unnamed) eastern form of *S. latrans* Hellmayr, which locally ascends the slopes through disturbed humid forest. On the western slopes it is replaced below in drier, more open scrub by *S. latrans subcinereus* Zimmer.

**Vocalizations.** The distinctive calls of *S. o. androstictus* are described above and shown in Fig. 3. In spite of this taxon's long genetic isolation and markedly different call, its song does not differ appreciably from that of *S. o. opacus* (Table 3; Figs. 1–2), except by lacking the 1–3 churring introductory notes found in 16 of 21 recordings of *opacus* (Fig. 5) and by sometimes being delivered without pause for two minutes or more, much longer than any recorded song of *S. o. opacus*. Usually, however, the song is 4–12 s long, as in nominate *S. opacus*. When *S. o. androstictus* in rare cases gives an introductory note, i.e. pauses after the first note, the note is of the same pitch and quality as the following notes. In vocalizations of both forms of *S. opacus* as well as in *S. canus*, the second, occasionally the first harmonic is loudest, and several more harmonics are often audible.

**Etymology.** The name refers to the white spot on the primary coverts found in most males, setting it apart from a nearby (Cordillera Colán, Amazonas, Peru) population, vocally unknown but presently referred to *S. parvirostris* Zimmer, in which a similar spot is found but in females only (Krabbe & Schulenberg 1997).

**Conservation.** Our revised classification of the *Scytalopus canus* complex has implications for conservation because a taxon that was formerly considered to represent a single species actually consists of three differentiated lineages. However, although they range over fairly small areas, there seems to be no immediate threat to the survival of any of them. The entire Ecuadorian part of the range of *S. opacus androstictus* lies within two large and continuous protected areas: Podocarpus National Park and Bosque Protector Colambo-Yacuri. Much of the range of *S. o. opacus* also lies within large national parks in Ecuador (e.g. Sangay, Llanganates, Cayambe-Coca) and Colombia (e.g. Los Nevados, Puracé). In the Western Andes of Colombia, *S. canus* is so far known to occur on Páramo de Paramillo, which is declared a national park, and Páramo de Frontino, of which only a small part is protected. It would be of interest to determine if it occurs on other paramos in the Western Andes, several of which are protected. The first one south of Frontino is entirely encompassed by a nature reserve, Farallones de Citará. It is separated from Frontino by a pass of 2200 m, higher than the lowest pass between Frontino and Paramillo (2150 m), so *S. canus* presumably also occurs here. Further south, the paramos are separated by passes lower than 1800 m. It would be of conservational interest to determine to what degree the range of *S. canus* coincides with that of *Coeligena orina* Wetmore, another bird confined to humid treeline scrub in the Western Andes and so far only recorded from Farallones de Citará and Frontino (Krabbe *et al.* 2005).



**FIGURE 5.** Beginning of song of northern *S. c. opacus* from Azuay, Ecuador, including two introductory notes. In southern *S. c. opacus* there is usually no introductory note and if present, it is of the same pitch and quality as the following notes.

**Biogeography.** It remains to be determined if *S. canus* evolved *in situ* or arrived to the northern end of Western Andes from the south, or through dispersal from the Central Andes across the Cauca Valley (see discussion in Krabbe *et al.* 2006). If it came from the south, it seems likely that all the highest paramos in this cordillera hold populations.

The restricted range of *S. o. androstictus* in the Andes in northernmost Peru and southernmost Ecuador closely matches that of *Metallura odomae* Graves, which is also replaced by a close relative (*M. williami atrigularis* Salvin) north of the Río Zamora. Three other forms, *Grallaria ridgelyi* Krabbe *et al.*, *Thryothorus euophrys atriceps* (Chapman), and a yet undescribed subspecies of *Synallaxis unirufa* Lafresnaye (J. V. Remsen & NK, unpubl. data) appear to have similar ranges, except that they also occur in forest down to ca. 2200 m and might range into the southern Cordillera del Cóndor (known to be the case for *Grallaria ridgelyi*; T. Mark, unpubl. data). The role of the ca. 10 km wide, dry Río Zamora valley as a dispersal barrier for treeline birds was first recognized by Robbins *et al.* (1994) and further discussed by Krabbe (2008). Three species, *Grallaricula lineifrons* (Chapman), *Anairetes agilis* (Sclater) and *Urothraupis stolzmanni* Taczanowski & Berlepsch, all confined to humid treeline scrub, have never been reported south of the Río Zamora despite presence of seemingly suitable habitat to the south. In contrast, some species occupying this habitat range across both sides of the Río Zamora (e.g. *Buthraupis wetmorei* R.T. Moore and *eximia* Boissonneau, evidence that different species respond differently to landscape features and historical events in the Andes.

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