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RESEARCH ARTICLE

Untangling cryptic diversity in the High Andes: Revision of the *Scytalopus* [*magellanicus*] complex (Rhinocryptidae) in Peru reveals three new species

Niels K. Krabbe,[1,*] Thomas S. Schulenberg,[2,3] Peter A. Hosner,[1,4,5,6] Kenneth V. Rosenberg,[2,3,7] Tristan J. Davis,[2] Gary H. Rosenberg,[2] Daniel F. Lane,[2] Michael J. Andersen,[4,8] Mark B. Robbins,[4] Carlos Daniel Cadena,[9] Thomas Valqui,[2,10,11] Jessie F. Salter,[2] Andrew J. Spencer,[3] Fernando Angulo,[10] and Jon Fjeldså[1,6]

[1]Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark
[2]Louisiana State University Museum of Natural Science and Department of Biological Sciences, Baton Rouge, Louisiana, USA
[3]Cornell Lab of Ornithology, Cornell University, Ithaca, New York, USA
[4]University of Kansas Biodiversity Research Institute, Lawrence, Kansas, USA
[5]Division of Birds, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA
[6]Center for Macroecology, Evolution, and Climate, University of Copenhagen, Copenhagen, Denmark
[7]American Bird Conservancy, The Plains, Virginia, USA
[8]Department of Biology and Museum of Southwestern Biology, University of New Mexico, Albuquerque, New Mexico, USA
[9]Laboratorio de Biología Evolutiva de Vertebrados, Departamento de Ciencias Biológicas, Universidad de los Andes, Bogotá, Colombia
[10]CORBIDI, Calle Sta Rita 105, of 02, Surco, Lima, Peru
[11]Universidad Nacional Agraria La Molina, Faculty of Forestry Sciences, Lima, Peru
*Corresponding author: nkkrabbe@gmail.com

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ABSTRACT

Tropical mountains feature marked species turnover along elevational gradients and across complex topography, resulting in great concentrations of avian biodiversity. In these landscapes, particularly among morphologically conserved and difficult to observe avian groups, species limits still require clarification. One such lineage is *Scytalopus* tapaculos, which are among the morphologically most conserved birds. Attention to their distinctive vocal repertoires and phylogenetic relationships has resulted in a proliferation of newly identified species, many of which are restricted range endemics. Here, we present a revised taxonomy and identify species limits among high-elevation populations of *Scytalopus* tapaculos inhabiting the Peruvian Andes. We employ an integrated framework using a combination of vocal information, mitochondrial DNA sequences, and appearance, gathered from our own fieldwork over the past 40 yr and supplemented with community-shared birdsong archives and museum specimens. We describe 3 new species endemic to Peru. Within all 3 of these species there is genetic differentiation, which in 2 species is mirrored by subtle geographic plumage and vocal variation. In a fourth species, *Scytalopus schulenbergi*, we document deep genetic divergence and plumage differences despite overall vocal similarity. We further propose that an extralimital taxon, *Scytalopus opacus androstictus*, be elevated to species rank, based on a diagnostic vocal character. Our results demonstrate that basic exploration and descriptive work using diverse data sources continues to identify new species of birds, particularly in tropical environs.

Keywords: integrated taxonomy, Neotropics, systematics, tapaculo, vocalizations

Desentrañando la diversidad críptica altoandina: revisión de *Scytalopus* [*magellanicus*] (Rhinocryptidae) en Perú revela tres nuevas especies

RESUMEN

Las zonas montañosas tropicales se caracterizan por un alto grado de reemplazo de especies a través de gradientes altitudinales y de topografías complejas, lo cual se manifiesta en una alta concentración de diversidad aviar. En estos paisajes, particularmente en grupos aviares con morfología conservada y difíciles de observar, los límites entre especies aún requieren ser aclarados. Uno de estos linajes es el género *Scytalopus*, que reúne a algunas de las aves con morfología más conservada. Estudios enfocados en las diferencias en repertorio vocal y relaciones filogenéticas han conducido a una proliferación de descripciones de especies nuevas, muchas de las cuales son endémicas con distribuciones muy restringidas. Presentamos una revisión taxonómica e identificamos límites de especies entre poblaciones de *Scytalopus* de grandes elevaciones de los Andes peruanos. Empleamos un enfoque integrado que combina información de vocalizaciones, de secuencias de ADN mitocondrial y de caracteres del plumaje.

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Los datos fueron obtenidos mediante nuestro trabajo de campo en los últimos 40 años, complementados con información de archivos de sonidos y especímenes de museo. Describimos tres nuevas especies endémicas de Perú. Dentro de las tres existe diferenciación genética, que en dos casos se asocia con variación geográfica sutil en plumaje y vocalizaciones. Documentamos que en una cuarta especie, *Scytalopus schulenbergi*, existe divergencia genética profunda y variación en plumaje a pesar de que las poblaciones son similares vocalmente en general. Además, proponemos que un taxón de otra región, *Scytalopus opacus androstictus*, se eleve al rango de especie, con base en un carácter vocal diagnóstico. Nuestros resultados demuestran que las exploraciones básicas y un trabajo descriptivo basado en fuentes de datos diversos sigue permitiendo identificar nuevas especies de aves, particularmente en ambientes tropicales.

Palabras clave: taxonomía integrada, Neotrópicos, sistemática, tapaculo, vocalizaciones

INTRODUCTION

The tropical Andes of South America are renowned for their high avian species richness. More so than anywhere else on Earth, this region has continued to be a reliable source of newly described bird taxa (Brewer 2018). Avian richness in the Andes is attributed to complex montane topography resulting in high species turnover. Such turnover is produced and maintained via 2 phenomena: (1) elevational replacement, whereby species occupy elevational zones with habitat bands dictated by temperature and precipitation gradients (Terborgh 1977, Rahbek 1997); and (2) allopatric replacement, whereby closely related species occupying similar elevations are isolated from one another by geographic barriers (e.g., Chapman 1926, Remsen 1984, Graves 1985, 1988).

In the Neotropics, perhaps no avian group exemplifies species turnover more than tapaculos in the genus *Scytalopus*, which inhabit forest understory and shrubby alpine habitats. All species skulk in dense vegetation, are poor fliers, and are reluctant to cross habitat gaps, making them unusually poor dispersers prone to population isolation. They inhabit mountains and foothills in Central America and the Atlantic Forest, but their diversity is greatest in the Andes. Along much of the humid Amazonian slopes of the Andes and parts of the humid Pacific slope of Colombia and Ecuador, multiple species replace each other elevationally with little or no local overlap (Cadena and Céspedes 2020). Elsewhere, such as in Bolivia, Venezuela, and parts of western Ecuador and Peru, there are fewer species and their elevational ranges are broader. That as many as 6 species can replace each other elevationally along the Amazonian slope in central Peru was shown by the discovery of *Scytalopus gettyae* (Hosner et al. 2013), together with later evidence (xeno-canto.org; XC229596) that *S. parvirostris* occurs rarely or locally on the same slope. Otherwise, species replacement occurs geographically across topographic barriers, most often deep, dry valleys (Arctander and Fjeldså 1994, Cadena and Céspedes 2020).

Tapaculo species are morphologically so conserved that many individuals are not reliably identified by external appearance alone (Krabbe and Schulenberg 1997). A few uniformly blackish species notwithstanding, most are overall grayish in plumage with rufous-and-black barring on the flanks and tail. In addition to the lack of diversity in adult plumages, many species seem to proceed through a prolonged (but poorly understood or documented) series of molts before reaching definitive plumage, rendering species identification solely on plumage characters even more difficult. Some taxa have distinctive white markings on the head or wings, but these markings are individually variable and are lacking in some individuals (Krabbe and Schulenberg 2003, Krabbe and Cadena 2010). As is typical of cryptically plumaged birds, they are most often detected and identified by their vocalizations.

Morphological homogeneity combined with fine-scale endemism and remote distributions have produced a gross underestimation of *Scytalopus* species, as well as a confused taxonomic history (Zimmer 1939, Krabbe and Schulenberg 1997, Cadena et al. 2020). Increases in numbers of recognized species are attributable to precise attention to elevational replacements of populations that differ in vocalizations (Fjeldså and Krabbe 1990, Whitney 1994, Krabbe and Schulenberg 1997) and to fine-scale geographical comparisons of genetics and voice (e.g., Cuervo et al. 2005, Maurício et al. 2008). The basis for these revisions are museum specimens conscientiously collected with voucher audio recordings so that plumage, voice, and genetics can all be tied to specific populations with confidence. As a result, recognized species diversity has risen dramatically from 10 (Peters 1951) to 44 (Gill and Donsker 2019, Remsen et al. 2019). Nevertheless, because of the limited in-depth work done to date with all data components needed for precise analysis, the true diversity within *Scytalopus* surely remains underestimated.

During his extensive *Scytalopus* revisions, Zimmer (1939) first realized that small-bodied tapaculo populations occupying the highest Andean elevations formed a cohesive group, hereafter referred to as "*S.* [*magellanicus*]". He consolidated these taxa, previously recognized as separate species (Chapman 1915, Cory and Hellmayr 1924), and described additional geographic variants (Zimmer 1939, 1941). As such, *S.* [*magellanicus*] constituted a polytypic species spanning the length of the Andes from Colombia to Tierra del Fuego. Zimmer's *S.* [*magellanicus*] group has been largely supported by molecular study, although most forms are now ranked as species (Krabbe and Schulenberg

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1997, Gill and Donsker 2019, Remsen et al. 2019, Cadena et al. 2020). When omitting *S. griseicollis*, which belongs in a separate clade (see Avendaño et al. 2015, Cadena et al. 2020), *S.* [*magellanicus*] is a monophyletic group comprising nearly a quarter of *Scytalopus* taxonomic diversity: 10 species with 2 additional described subspecies. Most forms replace each other geographically, although 2 species (*S. schulenbergi*, *S. fuscus*) are parapatric with other *S.* [*magellanicus*] members, replacing them elevationally or in different habitats.

Through central Peru, the humid forests and punas of the eastern Andes are bisected by an impressive series of dry valleys and canyons with depths of up to 3,000 m. Across this landscape, Zimmer (1939) had precious little *S.* [*magellanicus*] material to compare. Beginning in the 1970s, our fieldwork investigated sites in this region, often focusing on areas where humid montane forests and puna grasslands persist. In the 1980s we identified 2 vocally distinct *S.* [*magellanicus*] taxa, to which no name clearly applied. These populations were initially depicted by Fjeldså and Krabbe (1990; Unnamed ssp. Nev. Ampay, Apurímac, PLATE XLI 1h, page 440; Unnamed ssp. Millpo, Pasco, pages 440–441), and subsequently included in a series of publications (Arctander and Fjeldså 1994, Krabbe and Schulenberg 1997, 2003, Baldwin and Drucker 2016). Colloquially, these populations have been called "Ampay Tapaculo" and "Millpo Tapaculo" by birdwatchers for decades, but neither taxon has been described. Further explorations have uncovered *S.* [*magellanicus*] populations throughout the region, documenting that the species complex occurs nearly uninterrupted in suitable habitats across Peru (Hosner et al. 2015). Through the course of studying and analyzing *Scytalopus* vocalizations to formally describe Peruvian taxa, we detected a third unnamed *S.* [*magellanicus*] that is parapatric with *S. altirostris* in north-central Peru. Remarkably, a spectrogram of this third species' song was also illustrated in Fjeldså and Krabbe (1990), although it was mistakenly believed to represent *S. altirostris* ("*altirostris* Carpish mts", page 441) at that time.

More than 40 yr after our collective interests and fieldwork on *S.* [*magellanicus*] began, a wide sampling of *Scytalopus* vocalizations, combined with DNA sequences from modern and historic specimens, have clarified many of their systematic relationships (Cadena et al. 2020). Here, we present a revised taxonomy in an integrated framework, establishing species limits among high-elevation populations of *Scytalopus* tapaculos inhabiting the Peruvian Andes (Figures 1 and 2). We provide formal descriptions of 3 new species, all endemic to Peru. We also discuss geographic variation within described species, and highlight remaining knowledge gaps to concentrate future efforts.

METHODS

Fieldwork and Study Sites

The fieldwork was carried out through large parts of the central Peruvian Andes between 1978 and 2018. Details on study sites, dates, and individual authors' participations are given in Appendix C.

Vocal Comparisons

We downloaded sound recordings from throughout Peru from Macaulay Library (ML; www.macaulaylibrary.org) and xeno-canto (XC; www.xeno-canto.org), and supplemented these with a few uncatalogued recordings (Appendix B). We produced sonograms (spectrograms and oscillograms) and quantified vocal characteristics using CoolEditPro (Syntrillium Software, Scottsdale, AZ, USA).

The songs of members of *S.* [*magellanicus*] are almost as diverse as those across the remainder of the genus, ranging from repeated simple single notes or phrases to accelerating or decelerating, rising or falling phrases, rapid trills, and more complex, rhythmic phrases with several types of notes. Some species, including *fuscus*, *schulenbergi*, and heretofore unnamed birds from Apurímac and Ayacucho, have 2 song types: one given more often (primary song), the other given less frequently (secondary song). Excluding the distinctive songs of *S. opacus*, and *S. schulenbergi*, primary or secondary *S.* [*magellanicus*] songs throughout Peru are composed of series of stereotyped, regularly repeated phrases that we refer to as "churrs".

Within the greater part of each churr, the pitch rapidly oscillates between a high and low frequency at constant pace. We define each high-low-high or low-high-low oscillation as a "stroke" ("down-up-stroke" or "up-down-stroke"). Churrs vary markedly in their metrics across *S.* [*magellanicus*]. Specifically, we quantified 5 variables (Figure 3): churr pace (number of churrs per second), churr duration (not including pauses between churrs), number of strokes per churr (including irregular strokes), pace of strokes (excluding irregular introductory or terminal strokes), and frequency at maximum volume (kHz). The primary song of *Scytalopus* [*magellanicus*] populations inhabiting Ayacucho and Apurímac is composed of a repeated simple downstroke. For these single-noted songs we measured the pace of notes, note duration (from the beginning to the end of a note), and frequency at maximum volume (kHz). For churr songs and single-noted songs, we separately performed principal components analysis to assess whether taxa occupy unique areas of multivariate space using the native *prcomp* function in R 3.5 (R Core Team 2013). *Scytalopus opacus* and *S. schulenbergi* were not included in these quantifications because their songs are structured differently.

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FIGURE 1. New *Scytalopus* taxa from the Peruvian Andes. (*Upper left*) Adult male and female of Jalca Tapaculo, *Scytalopus frankeae* from Huánuco. (*Upper right*) Male *Scytalopus frankeae* from Junín. (*Lower left*) Adult males of Ampay Tapaculo, *Scytalopus whitneyi* (left from Apurímac, right from Ayacucho). (*Lower right*) Adult male (top) and female (below) of White-winged Tapaculo, *Scytalopus krabbei*. Watercolor painting by JF.

Morphological Comparisons

We performed visual assessments of plumage and took morphological measurements from *Scytalopus* [*magellanicus*] specimens from central and southern Peru (Appendix A). DFL took additional measurements (bill depth) from many of the same specimens as well as from some material in AMNH and USNM. Most specimens were gathered together for assessment at LSUMZ, but a few specimens were reviewed and measured separately by PAH and MBR. We measured wing (flat), tail, tarsus, and bill (from distal edge of the operculum to tip and depth at base). In addition to comparing measurements individually, we also performed principal components analysis to determine if taxa occupy unique areas of multivariate space using the *prcomp* function in R 3.5 (R Core Team 2013). We described plumage coloration using Munsell Soil Color Charts (1994, 2000).

Molecular Identification and Phylogeny

A comprehensive *Scytalopus* phylogeny based on mitochondrial NADH dehydrogenase 2 (ND2), ultraconserved elements (UCEs), and exon sequences was recently completed by Cadena et al. (2020). We sequenced 16 older *Scytalopus* specimens lacking vocal data, including the holotype of *S. altirostiris* (ANSP 115273 from Atuén, Amazonas), and we obtained ND2 sequences using methods designed for UCE capture and sequencing, to confirm their identities by comparison with the Cadena et al. (2020) reference database.

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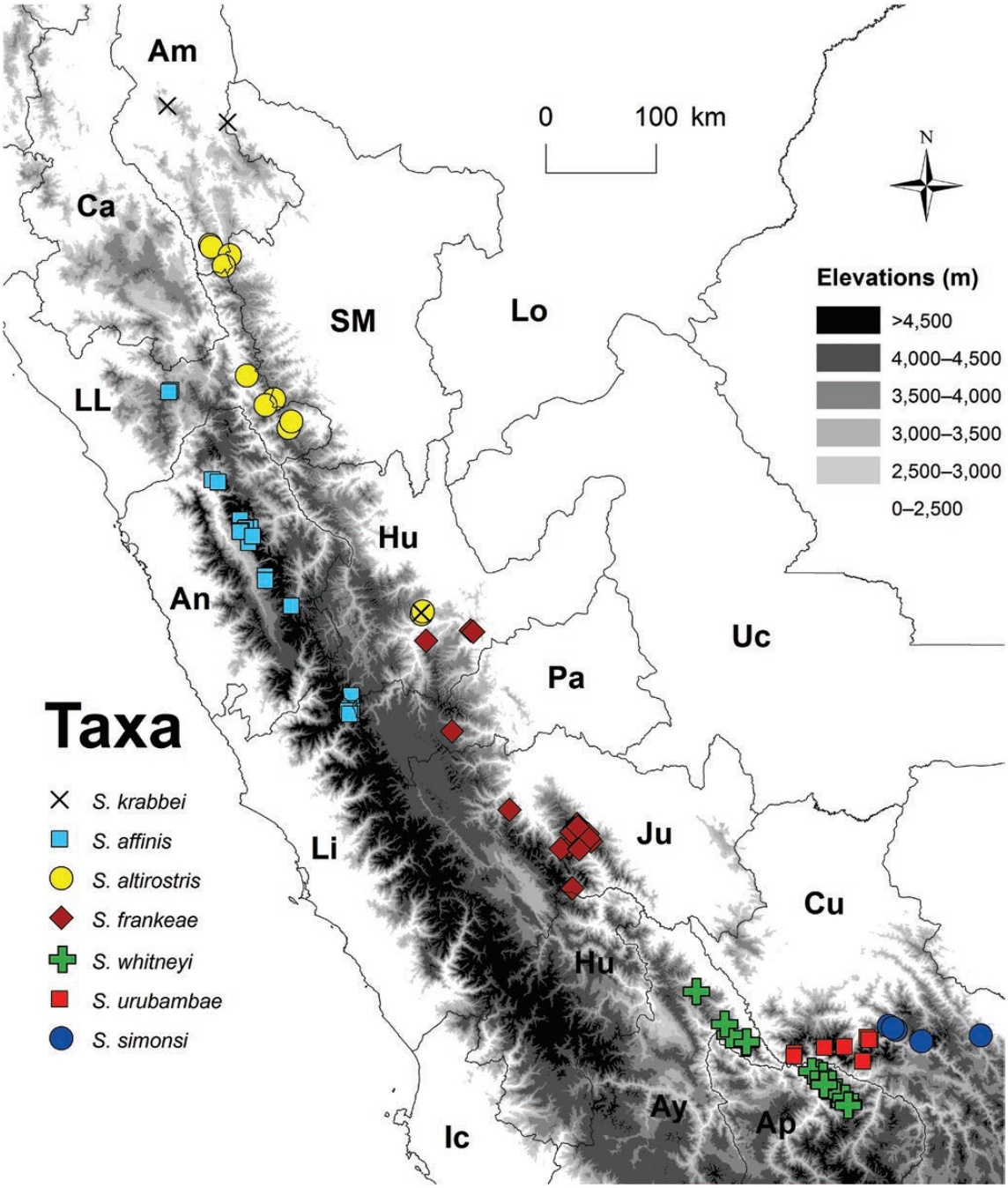

FIGURE 2. Known localities for central Peruvian forms in *Scytalopus* [*magellanicus*]. Names of departments abbreviated.

Briefly, we sampled dried tissue from specimen toepads and prepared them for sequence capture and Illumina sequencing following Salter et al. (2019). From demultiplexed samples, we quality-controlled reads using Trimmomatic (Bolger et al. 2014) default settings, and then readmapped to putative conspecific *Scytalopus* ND2 sequences in Geneious 6 (Kearse et al. 2012). Following readmapping, we checked sequence quality manually and extracted consensus ND2 sequences. Nine of these 16 specimens were confirmed to be *S.* [*magellanicus*] sequences (GenBank accession numbers MN729326-34), and were added to the 56 individuals previously sequenced (Cadena et al. 2020) along with 2 outgroup species (*S. acutirostris*, *S. diamantinensis*), totaling 66 sequences. This alignment represented all named taxa in *S.* [*magellanicus*] as well as unassigned populations from central Peru.

From the new combined dataset, we inferred a ND2 genealogy using maximum likelihood (ML, RAxML, Stamatakis

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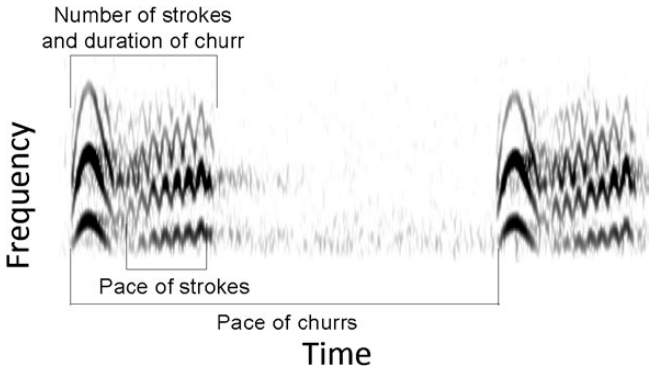

FIGURE 3. Section of song of *Scytalopus simonsi* with indications of the parts used for measuring pace of churrs, pace of strokes, number of strokes, and duration of churrs.

et al. 2014) and Bayesian (BEAST 2.2, Bouckaert et al. 2014) methods. Testing for sequence model fit in partitionFinder 2.1.1 (Guidon et al. 2010, Lanfear et al. 2012, 2016) considering all BEAST models, the AIC_c criterion, and the greedy search scheme identified the HKY+I+G, TRN+I+G, and GTR+I+G models for each codon position, respectively. However, in RAxML, we instead implemented an ML search and 1,000 rapid bootstraps using the GTR+ Γ model for each codon as recommended by the program authors; see also Abadi et al. (2019). For BEAST, we implemented 2 independent Markov chain Monte Carlo (MCMC) chains of 10 million generations, sampled every 10,000 generations, and chose a Birth-death tree prior. Preliminary MCMC runs using partitionFinder-identified sequence evolution models and an uncorrelated lognormal relaxed clock did not converge, suggesting overparameterization. For subsequent MCMC runs, we instead chose simpler HKY+I (1st–2nd positions) or HKY+Γ (3rd position) substitution models and a strict molecular clock (Ho and Duchêne 2014). We assessed parameter stationarity with Tracer 1.7 (Rambaut et al. 2018), and ensured that effective sample sizes for all parameters were greater than 200. After discarding the first 25% as burn-in, posterior trees were summarized as a maximum clade credibility tree with TreeAnnotator 2.2 (Bouckaert et al. 2014).

Taxonomy

We rank populations of *Scytalopus* as species when cumulative evidence supports that they are diagnosable, independently evolving lineages (de Queiroz 2007), which are likely reproductively isolated from each other. In practice, we apply information from vocal behavior, genetics, and morphology to assess whether populations consistently fulfill expectations characteristic of currently recognized *Scytalopus* species under different species concepts; more fulfilled criteria produce stronger and more comprehensive arguments for species rank. (1) Populations are found in sympatry or parapatry along elevational gradients without evidence of interbreeding, thus maintaining their integrity because of reproductive isolation (Mayr 1942). (2) Populations are vocally diagnosable. *Contra* Krabbe and Schulenberg (1997, 2003), who considered only vocal differences in song, we follow the broader approach by Whitney et al. (2010) by also including diagnostic calls. (3) Populations are genetically distinct, as inferred by phylogenetic analysis of available genetic data revealing reciprocal monophyly. We expect that populations are more likely to be species if they have maintained DNA sequence divergence from other similar populations, but we apply no operational thresholds for recognizing species. (4) Populations are morphologically diagnosable. Many universally accepted *Scytalopus* species fail to fulfill this expectation, but we include it for cases of morphological distinctness. Here, we rank populations as species if they fulfill at least criterion 1, or the union of criteria 2 and 3, resulting in taxonomic decisions broadly consistent with those already in place for *Scytalopus*, as for example with recognition of Diamantina Tapaculo *Scytalopus diamantinensis*, which is diagnosable genetically and by call, but essentially identical in adult plumage, and similar in song, to the allopatric Planalto Tapaculo *Scytalopus pachecoi* (Gill and Donsker 2019, Remsen et al. 2019).

RESULTS

Systematic Relationships

Bioacoustic, phylogenetic, and to some extent morphological data demonstrate distinct geographical structure of *Scytalopus* [*magellanicus*] throughout Peru. We identified strongly supported mtDNA clades corresponding to currently recognized species *S. opacus, S. altirostris, S. affinis, S. simonsi,* and *S. urubambae,* and 3 unnamed lineages that are geographically circumscribed: 1 from Amazonas, San Martín, and Huánuco north of the Río Huallaga (northern); 1 from Huánuco south of the Río Huallaga, Pasco, and Junín (central); and 1 from Ayacucho and Apurímac (southern). Each of these clades was vocally diagnosable (Figures 4 and 5, Table 1), and most were identifiable by adult male plumage characters and bill measurements (Tables 2 and 3). One or more of the 5 vocal characters that varied among these taxa diagnosed all recognized species (*S. altirostris, S. affinis, S. urubambae, S. simonsi*) and unnamed populations with "churr" songs. Similarly, these species and unnamed populations generally occupied separate portions of churr song principal component analysis (PC)-space (Appendix Figure 7).

Unexpectedly, we recovered no statistical support for the monophyly of *S. schulenbergi* because a *S. schulenbergi* specimen from Cusco was strongly divergent from specimens from Puno and La Paz, Bolivia. Consequently, analyses were unable to resolve ND2 relationships among *S. schulenbergi* (Puno/La Paz), *S. schulenbergi* (Cusco), *S. urubambae*, and the southern unnamed population (Ayacucho and Apurímac). Our phylogenetic analysis revealed that the type specimen of *S. altirostris* from Atuén,

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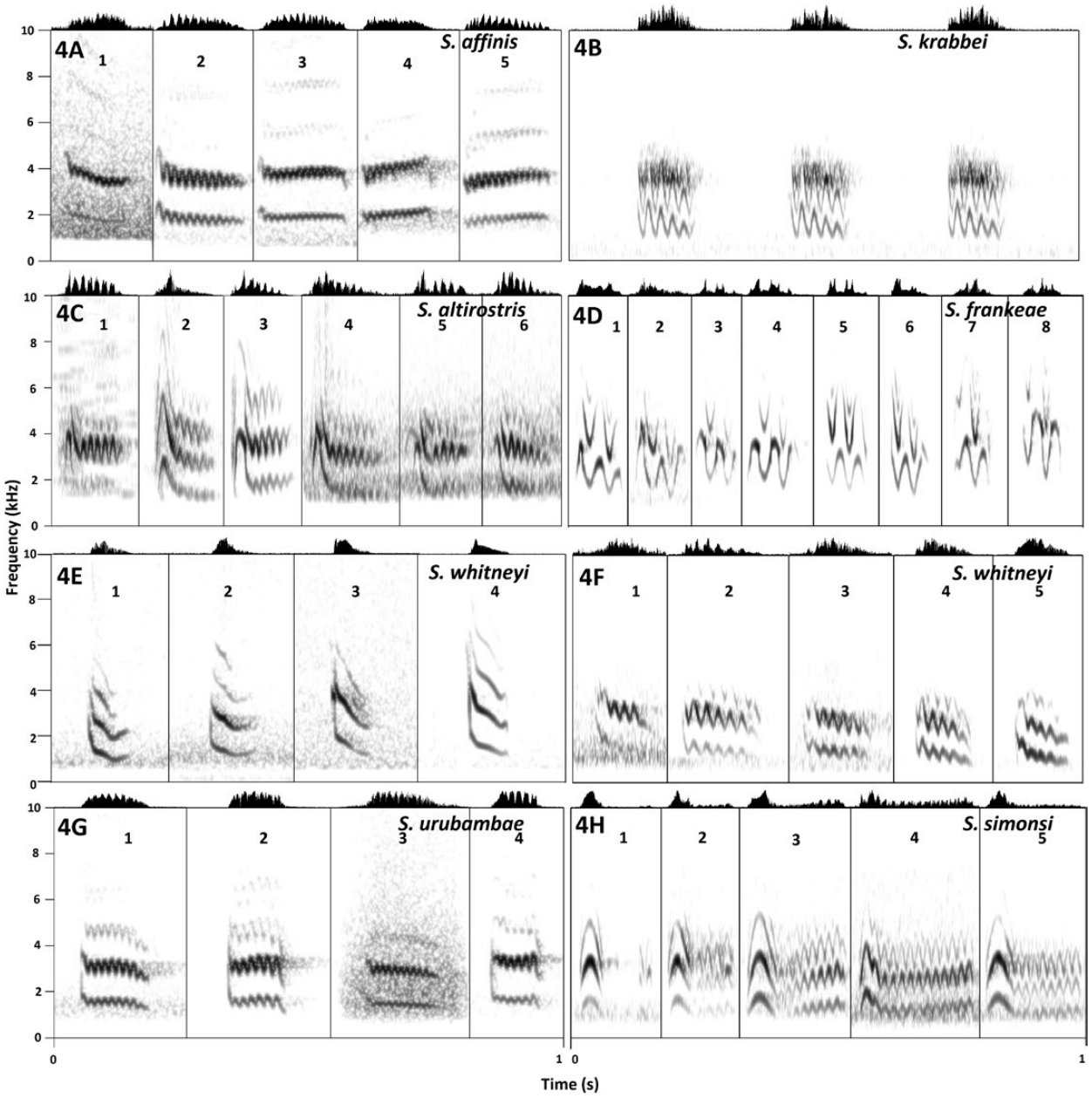

FIGURE 4. Sonograms of churrs from songs of most Peruvian members of *Scytalopus* [*magellanicus*]. Songs are up to several minutes long and are composed of regularly repeated churrs. **(A)** Single churrs from songs of 5 individuals of *S. affinis*. Panel 1: ML208624, panel 2: XC43688, panel 3: XC153754, panel 4: XC229436, panel 5: XC387836. Panel 3 is from Huánuco, the rest from Ancash. Note the variability in frequency amplitude of individual strokes and in general change of pitch. **(B)** Section of song of *S. krabbei* Huánuco (XC20182). Song recorded in Amazonas and northern San Martín is similar. The strong resonance at 3,100–4,400 Hz gives the churrs a distinctive rattling quality. The pace of churrs is much faster than in any of the other forms shown. **(C)** Churrs from song of 6 individuals of *S. altirostris*. Panel 1: central San Martín (XC147); panels 2–3: southern Amazonas (XC40729, XC115772); panel 4: southern San Martín (XC468094); panels 5–6: Huánuco (XC229437a,b). All have a distinct introductory note, but change in average pitch of the rest of the churr varies. **(D)** Churrs from songs of 8 individuals of *S. frankeae*. Panels 1–4 from Huánuco (panel 1: ML36058, panel 2: ML40130, panel 3: ML195139, panel 4: ML195147), panels 5–8 from Junín (panel 5: ML171881, panel 6: XC20431, panel 7: XC20666, panel 8: XC41106). Note that songs from Junín are shortest and usually begin with a downstroke. **(E)** Single notes from primary songs of 4 individuals of *S. whitneyi*. Panel 1 (ML129544) and panel 2 (ML230279, holotype) are from Apurímac, panel 3 (ML186900) and panel 4 (ML186901) from Ayacucho. **(F)** Churrs from secondary song of 5 individuals of *S. whitneyi*. Panel 1 from Ayacucho (ML186928), panels 2–5 from Apurímac (panel 2: XC33861, panel 3: XC333300, panel 4: XC36107, panel 5: ML129545). **(G)** Churrs from songs of 4 individuals of *S. urubambae*. Panel 1: ML173950; panel 2: ML186970; panel 3: XC468100; panel 4: XC73813. Note variation in change of pitch and in frequency amplitude. **(H)** Churrs from songs of 5 individuals of *S. simonsi* from Cusco. Panel 1: ML516940, panel 2: XC92337, panel 3: XC229605, panel 4: ML59776901, panel 5: ML100969. Note the great relative volume of the introductory note and that the following churr may rise or be constant, but not fall in average pitch.

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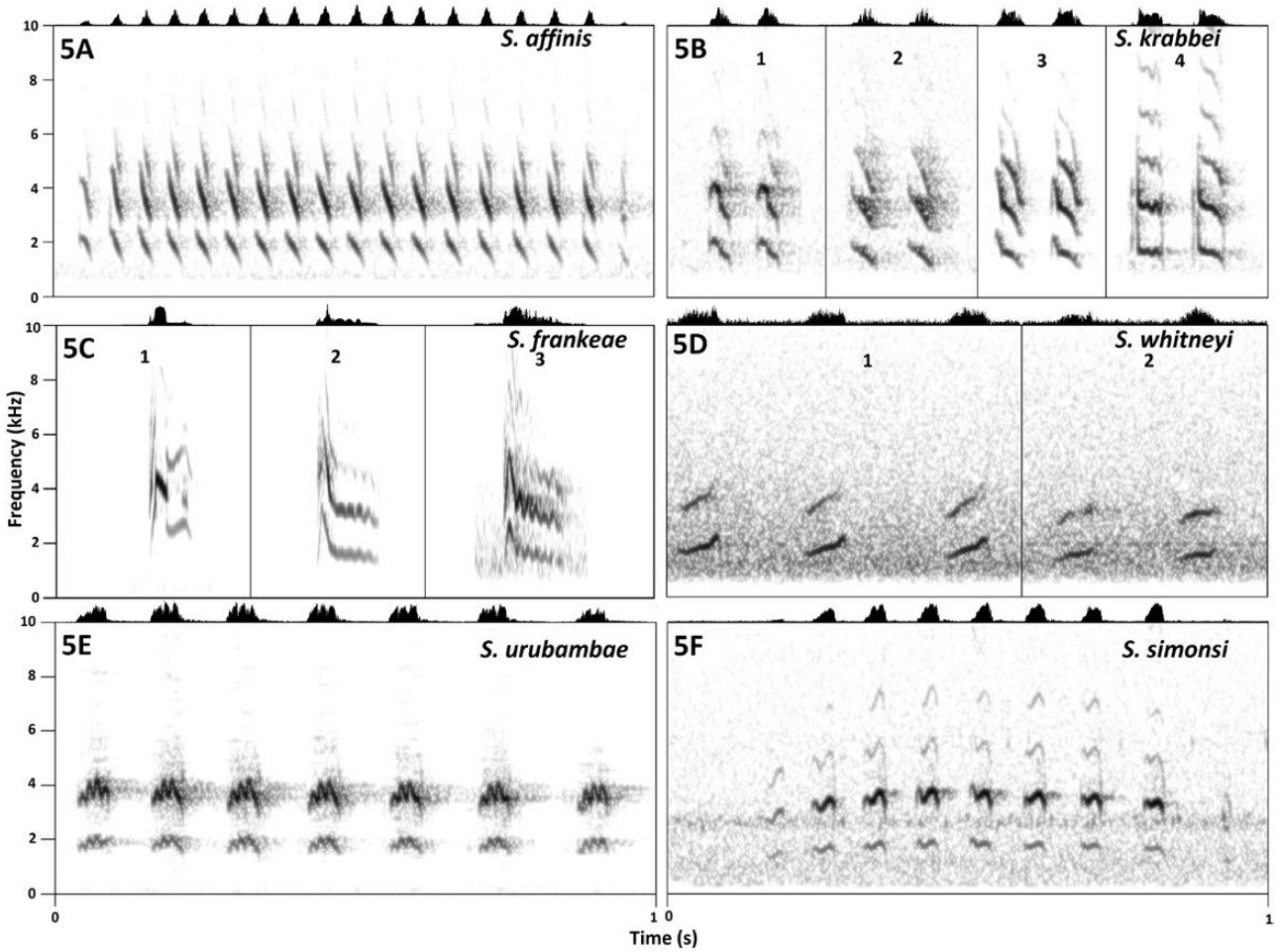

FIGURE 5. Sonograms of calls of members of *Scytalopus* [*magellanicus*] from central and south Peru. **(A)** Scold of *S. affinis* (ML11077). Note shape is similar in all 9 recordings examined. **(B)** Two notes from each of 1 s long scolding calls of similar notes by 4 individuals of *S. krabbei*. Panel 1 (ML531469, Holotype) and panel 2 (ML531470) from San Martín, panel 3 (XC46782) and panel 4 (ML104960821) from Huánuco. **(C)** Calls of *S. frankeae*. Panel 1: call by a presumed female (ML195147). Panel 2 (ML166389) and panel 3 (XC29837): single churrs presumed to be given by males. **(D)** Scolding calls of *S. whitneyi*. Panel 1: 3-noted (ML128964); Panel 2: 2-noted (ML128966). **(E)** Scold of *S. urubambae* (XC468104). Scolds are composed of 5–7 short churrs. Known to be given by females, but probably also by males. **(F)** Scold of *S. simonsi*. Cusco (ML143675).

Amazonas, Peru, grouped with a specimen referred to *altirostris* from Unchog, Huánuco, and was only distantly related to a vocally distinct population also traditionally thought to represent *altirostris* and occurring in Amazonas, San Martín, and Huánuco north of the Río Huallaga (Cadena et al. 2020). The affinities of the *S. altirostris* type confirm that the latter population represents a third undescribed and unnamed taxon.

Each of the 3 unnamed populations fulfills criteria expected of *Scytalopus* species. They are each vocally diagnosable and have monophyletic mitochondrial sequences. The northern population (Amazonas, San Martín, and Huánuco north of the Río Huallaga) is identifiable by plumage characteristics and morphological measurements, and occurs locally in parapatry with *S. altirostris*. The central population is distinguishable from *S. altirostris* genetically and vocally but not in morphology or plumage. The southern population is also identifiable by plumage characteristics. We formally describe these 3 species here.

Scytalopus krabbei sp. nov.
[T. S. Schulenberg, D. F. Lane, A. J. Spencer, F. Angulo, and C. D. Cadena]
White-winged Tapaculo

Holotype

LSUMZ 174041; adult male, collected by Daniel F. Lane (DFL 1753) in humid temperate shrub forest on June 29, 2002, in Peru: San Martín/Amazonas border: east slope of Cerro Patricia, ~22 km ENE of Florida, Camp Buena Vista Social Club, Bosque de Proteccion Alto Mayo, coordinates: 5.723°S, 77.754°W, elevation: 2,975 m. Vocalizations audio

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TABLE 1. Some measurements (range, mean ± SD, number of individuals sampled) of songs of some members of *Scytalopus* [*magellanicus*] from Peru and immediately adjacent Bolivia. Note the rapid pace of *krabbei*, the few and slow-paced strokes in churrs of *S. frankeae*, birds from Junín with fewest strokes and highest pitch. Note also the single-noted song of *S. whitneyi*, highest pitched in birds from Ayacucho. The slow-paced strokes and high pitch in churred song from Ayacucho (*n* = 1) might also prove to be a constant difference from Apurímac birds.

	Pace of churrs (churrs s^{-1})	Duration of churr (s)	Number of strokes in churr	Pace of strokes in churr (strokes s^{-1})	Loudest pitch of churr (Hz)	Pace of 1-noted song (notes s^{-1})	Duration of note in 1-noted song (s)	Loudest pitch of 1-noted song (Hz)
S. affinis	2.2–3.8 (3.2 ± 0.5) *n* = 18	0.11–0.18 (0.15 ± 0.02) *n* = 18	7–14 (11 ± 2) *n* = 18	69–91 (80 ± 7) *n* = 18	3,410–4,363 (3,770 ± 282) *n* = 18			
S. krabbei	3.8–5.5 (4.6 ± 0.9) *n* = 3	0.08–0.12 (0.10 ± 0.02) *n* = 3	5–6 (5.3 ± 0.6) *n* = 3	43–58 (51.3 ± 7.6) *n* = 3	3,332–3,902 (3,600 ± 287) *n* = 3			
S. altirostris	1.6–2.6 (2.1 ± 0.3) *n* = 10	0.10–0.14 (0.12 ± 0.01) *n* = 9	5.0–9.0 (6.7 ± 1.1) *n* = 9	61–79 (70 ± 6) *n* = 9	3,135–3,650 (3,456 ± 159) *n* = 10			
S. frankeae Huánuco	1.5–1.8 (1.7 ± 0.1) *n* = 7	0.08–0.12 (0.09 ± 0.01) *n* = 7	2.5–3.5 (2.9 ± 0.4) *n* = 7	25–31 (28 ± 2) *n* = 7	3,085–3,665 (3,413 ± 186) *n* = 7			
S. frankeae Junín	1.6–2.3 (1.9 ± 0.2) *n* = 6 [a]	0.05–0.08 (0.07 ± 0.01) *n* = 25	2.0–3.0 (2.5 ± 0.3) *n* = 25	26–36 (31 ± 2) *n* = 25	2,408–4,466 (3,877 ± 474) *n* = 25			
S. whitneyi Ayacucho	2.0 *n* = 1	0.12 *n* = 1	5.5 *n* = 1	39 *n* = 1	3,163 *n* = 1	1.5–1.8 (1.7 ± 0.1) *n* = 6	0.07–0.08 (0.07 ± 0.01) *n* = 6	3,129–3,729 (3,355 ± 241) *n* = 6
S. whitneyi Apurímac	1.6–2.2 (1.9 ± 0.2) *n* = 8	0.11–0.16 (0.12 ± 0.02) *n* = 7	5.0–6.5 (5.6 ± 0.5) *n* = 7	43–56 (50 ± 5) *n* = 8	2,604–3,144 (2,797 ± 205) *n* = 7	1.5–2.2 (1.9 ± 0.2) *n* = 18	0.05–0.11 (0.08 ± 0.01) *n* = 18	2,224–3,214 (2,860 ± 237) *n* = 18
S. urubambae	1.7–2.4 (2.0 ± 0.2) *n* = 12	0.10–0.15 (0.11 ± 0.02) *n* = 12	6–11 (7.4 ± 1.5) *n* = 12	60–82 (66 ± 6) *n* = 12	2,867–3,323 (3,131 ± 157) *n* = 12			
S. simonsi Cusco	1.6–2.3 (2.0 ± 0.3) *n* = 14	0.13–0.22 (0.16 ± 0.03) *n* = 13	3–13 (6.5 ± 2.9) *n* = 13	53–64 (58 ± 3) *n* = 13	2,636–3,520 (3,233 ± 259) *n* = 14			
S. simonsi Puno and *n* La Paz	1.7–2.7 (2.1 ± 0.4) *n* = 6	0.12–0.17 (0.15 ± 0.02) *n* = 6	5–9.5 (7.3 ± 1.6) *n* = 6	57–66 (60 ± 3) *n* = 6	3,391–3,722 (3,567 ± 128) *n* = 6			

[a] Natural song. Songs recorded after playback measured 1.9–2.7 (2.3 ± 0.2) *n* = 12. No effect of playback was evident for other variables.

recorded by Daniel F. Lane (ML531469/XC237624). Tissue samples preserved (LSUMZ B-43813). ZooBank registration A77E1A34-6D32-420B-9BE0-2C54E5769E0B; ND2 sequence GenBank MN692513.

Diagnosis

Scytalopus krabbei has long been confused with *S. altirostris*, but these 2 species differ from each other in many respects and are only distantly related to each other. Most noticeable, all known *S. krabbei* specimens have a small white wing patch formed by white outer webs of the outer 2 or 3 greater primary coverts, which differentiate it from all other *Scytalopus* except for some males of the allopatric *S. opacus androstictus* (Krabbe and Cadena 2010). Additionally, *S. krabbei* averages larger (Table 2), with a thinner bill throughout its length. By contrast, the base of the mandible is deep in *S. altirostris,* as its name indicates. *Scytalopus krabbei* lacks the whitish supercilium of *S. altirostris* and several other *S.* [*magellanicus*] species. The head, mantle, throat, and breast of fully adult *S. krabbei* are generally grayer and less brownish than those of *S. altirostris,* and its rump and back are less prominently barred. The tail of *Scytalopus krabbei* is dusky finely mottled with tawny markings, rather than clearly pale brown with dark barring or vermiculations as in *S. altirostris.* Outside of the *S.* [*magellanicus*] complex, *S. krabbei* differs from syntopic *S. acutirostris* from Huánuco and Amazonas in being lighter gray and in having brown flanks with sparse and relatively broad (1.4 mm) blackish barring, whereas specimens of *S. acutirostris* in this region have the flanks dark with little or no brown and no barring. The tail of *S. acutirostris* also differs from *S. krabbei* in being uniform blackish. The back of *S. krabbei* is usually paler and browner, but in fully adult specimens (including the holotype) it is as dark as in *S. acutirostris*. Within the Cordillera Colán in Amazonas department, *S. krabbei* differs from

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TABLE 2. Measurements (range, mean, standard deviation, and sample size) of specimens of central and south Peruvian members of *Scytalopus* [*magellanicus*]. Wing measure is of flattened wing, bill measure from fore edge of operculum to tip. There was no suggestion of mensural differences between *simonsi* from Cusco ($n = 3$ mm, 2ff) and Puno ($n = 10$ mm, 6ff).

Taxon	Sex	Weight (g)	Wing (mm)	Tail (mm)	Tarsus (mm)	Bill (mm)
affinis	mm	13–18.6 (15.3 ± 2.1), $n = 5$	50–57 (53.1 ± 2.7), $n = 7$	35–38.2 (37.0 ± 1.3), $n = 6$	18.2–22.8 (20.3 ± 1.7), $n = 7$	4.9–7.4 (6.3 ± 1.0), $n = 7$
krabbei	mm	18.0–20.8 (19.1 ± 1.5), $n = 3$	55–59 (57.0 ± 2.0), $n = 3$	36.8–40.8 (39.1 ± 2.1), $n = 3$	23.0–24.6 (23.9 ± 0.8), $n = 3$	5.8–6.5 (6.1 ± 0.4), $n = 3$
altirostris	mm	17–21 (18 ± 2), $n = 4$	47–59 (56 ± 4), $n = 9$	34–39 (36 ± 2), $n = 9$	18.9–21.8 (20.8 ± 0.9), $n = 9$	4.9–6.5 (5.8 ± 0.5), $n = 9$
Frankeae Huánuco	mm	16.5–19 (17.6 ± 0.7), $n = 19$	48–56 (53.9 ± 2.0), $n = 20$	26.8–36.7 (34.2 ± 2.3), $n = 20$	18.8–21.4 (20.3 ± 0.6), $n = 20$	5.4–6.6 (5.8 ± 0.3), $n = 20$
Frankeae Junín	mm	16.1–17.7 (16.9 ± 0.6), $n = 5$	51–54 (53.0 ± 1.2), $n = 5$	32.8–35.1 (33.8 ± 0.9), $n = 5$	17.7–20.8 (19.4 ± 1.4), $n = 5$	5.0–7.0 (5.9 ± 0.7), $n = 5$
whitneyi	mm	14.7–17.2 (15.6 ± 1.0), $n = 5$	47.2–53 (51.0 ± 2.0), $n = 8$	34.5–38.8 (37.3 ± 1.6), $n = 8$	18.6–20.8 (19.6 ± 0.7), $n = 8$	5.5–6.4 (5.9 ± 0.4), $n = 5$
urubambae	mm	14.6–16.9 (15.5 ± 0.9), $n = 5$	49–53 (50.9 ± 1.5), $n = 7$	32–38 (35.1 ± 2.5), $n = 6$	19–21 (20.2 ± 0.7), $n = 7$	4.6–5.7 (5.2 ± 0.6), $n = 3$
schulenbergi (Peru)	mm	12–17 (15.2 ± 1.5), $n = 8$	52–56 (53.9 ± 1.2), $n = 9$	31.5–40 (36.5 ± 2.9), $n = 9$	21.3–23.2 (22.1 ± 0.6), $n = 9$	5.4–6.2 (5.8 ± 0.2), $n = 9$
simonsi (Peru)	mm	15–17.2 (16.0 ± 0.7), $n = 10$	46–54 (51.7 ± 2.3), $n = 13$	34.6–42.2 (37.2 ± 2.4), $n = 12$	18.6–21 (20.2 ± 0.6), $n = 13$	5.1–6.5 (5.8 ± 0.4), $n = 9$
affinis	ff	16, $n = 1$	51–53 (52 ± 1), $n = 3$	32.6–37.4 (34.8 ± 2.4), $n = 3$	18.9–20.3 (19.5 ± 0.7), $n = 3$	6.1–6.4 (6.3 ± 0.2), $n = 2$
krabbei	ff	16.5–18 (17.2 ± 0.6), $n = 4$	54–61 (58.0 ± 3.2), $n = 4$	35.8–41.1 (37.7 ± 2.5), $n = 4$	22.5–25.8 (23.7 ± 1.5), $n = 4$	5.2–6.9 (6.2 ± 0.7), $n = 4$
altirostris	ff	21, $n = 1$	52–56 (54 ± 2), $n = 5$	31–38 (35 ± 3), $n = 5$	20.0–21.1 (20.4 ± 0.4), $n = 5$	5.0–6.2 (5.8 ± 0.5), $n = 5$
Frankeae Huánuco	ff	17–18 (17.4 ± 0.4), $n = 5$	52–57 (54.0 ± 1.7), $n = 9$	31.2–38.7 (35.1 ± 2.6), $n = 9$	19.4–22 (20.2 ± 0.8), $n = 9$	5.5–6.2 (5.9 ± 0.3), $n = 9$
Frankeae Junín	ff	13.7–17.4 (15.5 ± 1.4), $n = 5$	50–55 (52.5 ± 2.1), $n = 4$	31.3–33.3 (32.6 ± 1.1), $n = 3$	15.7–18.3 (16.9 ± 1.1), $n = 4$	5.9–7.5 (6.7 ± 0.8), $n = 4$
whitneyi	ff	14.2, $n = 1$	48, $n = 1$	31.2, $n = 1$	18.7, $n = 1$	5.5, $n = 1$
urubambae	ff	17.4, $n = 1$	53–55 (54 ± 1.4), $n = 2$	33–34 (33.5 ± 0.7), $n = 2$	18.8–20 (19.4 ± 0.8), $n = 2$	5.3, $n = 1$
schulenbergi (Peru)	ff	11.5–16 (14.1 ± 1.9), $n = 6$	50–54 (51.8 ± 2.1), $n = 4$	31.8–38.2 (35.8 ± 3.0), $n = 4$	21–23 (22.1 ± 1.0), $n = 4$	5.3–5.8 (5.5 ± 0.2), $n = 4$
simonsi (Peru)	ff	13–17 (15.1 ± 1.4), $n = 7$	49–57 (52.6 ± 2.7), $n = 7$	31.7–38.1 (34.9 ± 2.4), $n = 7$	18–21.5 (19.9 ± 1.1), $n = 7$	5.2–6.1 (5.6 ± 0.3), $n = 7$

presumed specimens of *S. parvirostris* (no voice recording is vouchered by a specimen) by having shorter tail and tarsi, slightly darker gray plumage, distinctly barred flanks, lacking broad pale feather tips on central underparts, and possessing a white spot in the wing. Pale belly feather tips are typical of *S. parvirostris* from the Cordillera Colán, but may at least sometimes be absent in *S. parvirostris* from the Carpish Mountains (Paty Trail) in Huánuco. When pale feather tips on the belly are present in *S. krabbei*, they are narrower than in *parvirostris* (1 vs. 2.5 mm). Apart from the white wing patch, *S. krabbei* is best diagnosed vocally (see below).

Description of Holotype

Forecrown, crown, and mantle dark gray (N3/0), feathers slightly darker distally, forming a faint scaled pattern. Lores and preocular area blackish. Lower back, rump, and upper tail coverts dark fuscous brown (10YR3/6), the upper tail coverts with 2 or 3 subterminal blackish transverse bars. Rectrices fuscous brown (10YR3/6) indistinctly barred with dusky; central rectrices only marked with dusky on edges of distal half. Outer web of 2 outer greater primary coverts white. Underparts dark gray (N3/0) slightly lighter than upperparts, flanks and under tail coverts dark yellowish brown (10YR3/6–4/6) with regular, ~1.4 mm wide, straight, dusky bars. Iris dark brown, bill slate black, tarsus and toes reddish brown. Left testis 2 × 4 mm. Mass 20.8 g. Ten rectrices. Stomach contained insect parts (saved). Skull unossified. No molt. Measurements (mm): wing (flat) 55, tail 40.8, tarsus 24.6, bill from fore edge of operculum 5.8.

Variation among Males

Two presumed subadult males (LSUMZ 74122 and 174042) are similar to the type except for having the crown and mantle dark brown; one also differs in having more extensive white on the primary coverts.

Description of Female

Four females (LSUMZ 88131, 88137, 88141, 88143) are similar to males, but have smaller body mass and average lighter gray (N4–5/0) and yellowish brown (10YR5–6/6) in coloration; the brown and dusky bars of the flanks extend onto the lower belly, and the bill and feet are lighter.

Vocalizations

Song (Figure 4B) 2–16 s long ($n = 3$), a series of regularly repeated churrs given at a pace of 3.8–5.5 s^{-1}. *Scytalopus krabbei* has the fastest pace of any churred song in *S.* [*magellanicus*] outside of *S. canus* and *S. schulenbergi*, which have differently structured songs. There is little or no overlap in song pace (4.6 ± 0.9) compared with its sister *S. affinis* (3.2 ± 0.5) or to the sympatric—but more distantly related—*S. altirostris* (2.1 ± 0.3) (Table 1). Churrs are composed of connected similar strokes that descend

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TABLE 3. Range, mean, standard deviation, and sample size for depth at base of bill (mm) of some Peruvian *Scytalopus* species (both sexes). Species abbreviations are: acuti = *acutirostris*, affin = *affinis*, krabb = *krabbei*, altir = *altirostris*, frank = *frankeae*, whitn = *whitneyi*, uruba = *urubambae*, simon = *simonsi*, and schul = *schulenbergi*. *Scytalopus simonsi* and *S. schulenbergi* specimens are from Cusco, Puno, and w La Paz. Note that all taxa overlap. The deepest bill measured was of *S. altirostris*, the thinnest of *S. acutirostris*.

acuti	affin	krabb	altir	frank	whitn	uruba	simon	schul
3.0–4.6	3.7–4.6	3.7–4.0	3.8–5.9	3.7–5.5	4.0–4.9	3.5–4.5	3.3–4.5	3.2–4.4
(4.0 ± 0.3)	(4.2 ± 0.3)	(3.9 ± 0.1)	(5.0 ± 1.0)	(4.5 ± 0.3)	(4.4 ± 0.3)	(4.0 ± 0.4)	(3.9 ± 0.3)	(4.0 ± 0.3)
n = 27	*n* = 11	*n* = 6	*n* = 15	*n* = 31	*n* = 5	*n* = 5	*n* = 25	*n* = 14

progressively in pitch, and have a distinctive rattling quality. In one recording (XC470184), the average pitch of churrs falls about 8 half notes during the first quarter of the song bout and then remains level, but in the 2 other recordings of song it remains level throughout. The scolding call (n = 6) is a distinctive 1 s long trill of 9–12 similar notes given at a pace of 10–13 s^{-1} with the loudest pitch at 3.2–3.9 kHz (Figure 5B, panels 1–4). Between 2009 and 2016, AJS made observations of *S. altirostris/S. krabbei* vocal behavior after playback of recorded materials. Without exception, birds responded aggressively to vocalizations of their own species, and ignored recordings of the congener.

Distribution

Known from 5 localities in 3 widely separated areas in the Central Andes of north-central Peru: Cordillera Colán in Amazonas (5.597°S, 78.245°W and approximately 5.55°S, 78.32°W); the type locality (Cerro Patricia) in northern San Martín near the Amazonas border (5.723°S, 77.754°W); and central Huánuco at Bosque Unchog (9.737°S, 76.170°W) and between Zapatagocha and Huaylaspampa (9.769°S, 76.085°W). It has been recorded at elevations ranging from 2,775 to 3,500 m, but primarily from 2,900 to 3,100 m. Although possibly absent locally as a result of interspecific competition, it is likely that *Scytalopus krabbei* occurs elsewhere along the humid eastern slope of the Andes north of the Río Huallaga. This region is remote and relatively little explored, and *S. krabbei* long has been confused with *S. altirostris*. The 2 are syntopic at Bosque Unchog, but *S. krabbei* is generally replaced at higher elevations by *S. altirostris*, a species that appears to be absent from both Cordillera Colán and Cerro Patricia. The altitudinal range of *S. krabbei* is entirely encompassed by the forest-based *S. acutirostris*, which also occurs at lower elevations. In northern San Martín, where *S. acutirostris* appears to be absent, *S. krabbei* may be replaced at lower elevations by *S. parvirostris*.

Habitat

Scytalopus krabbei has been recorded in wet shrub forest and upper montane forest. Where it co-occurs with *S. acutirostris*, *S. krabbei* may be more closely tied to actual shrubline vegetation where it interdigitates with open tussock grass habitat, whereas *S. acutirostris* is also found in deeper elfin forest understory.

Conservation

Scytalopus krabbei is common in appropriate habitat in the Bosque de Protección Alto Mayo (1,820 km^2) and Santuario Nacional Cordillera de Colán (392 km^2). Possibly, it is less common or local further south where known to be syntopic with *S. altirostris*. We suggest that it be categorized as a species of least concern (LC) in the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN 2019).

Etymology

The modern knowledge of the systematics of *Scytalopus*, including recognition of a level of diversity in the genus that would have astounded earlier generations of ornithologists, is largely due to Niels K. Krabbe, through his careful and thorough research both in the field and in the collection. Having himself contributed to the descriptions of no fewer than 7 new taxa of *Scytalopus*, we take great pleasure in taking the opportunity to name this new species in honor of our friend and colleague. The proposed English name refers to the small patch of white on the wing coverts, a feature—otherwise unusual in tapaculos—that is present on all known *S. krabbei* specimens.

Remarks

Populations from Huánuco and San Martín/Amazonas are 4.3–4.4% divergent in ND2 sequence (pairwise uncorrected difference). No phenotypic variation appears to coincide with this divergence, but available specimens and recordings are limited. Audio recordists should target *S. krabbei* from throughout its distribution for further study. *Scytalopus krabbei* meets all 4 of our criteria for the recognition of a species, and clearly qualifies for recognition under any species concept.

This species has been hiding in plain sight for decades. TSS assiduously collected *Scytalopus* during the entire Cordillera de Colán expedition (June–October 1978), at a time when species diversity in the genus was greatly underappreciated. No audio recordings were obtained during this expedition, so the entire Colán series has contributed little to revisions of *Scytalopus* that relied heavily on vocalizations (e.g., Krabbe and Schulenberg 1997). Nonetheless, it would have been reasonable to infer that specimens of *S.* [*magellanicus*] from Colán

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would represent *S. altirostris*, the type locality of which (Atuén) is a mere 140 km to the south-southeast. In 2002, DFL and TV encountered a *S.* [*magellanicus*] tapaculo at Cerro Patricia, a location southeast of Colán and north of Atuén, and obtained poor audio recordings. Again, it was easy to infer that the Cerro Patricia population was the same as that at both Colán and Atuén, although DFL was aware that the birds at Cerro Patricia had a different song than that attributed to *S. altirostris* from elsewhere in its range (Schulenberg et al. 2010). We turned greater attention to these birds when preliminary genetic data by CDC revealed that samples identified as *S. altirostris* from Cerro Patricia and from Bosque Unchog represented 2 divergent lineages (Cadena et al. 2020). This surprising discovery set in motion 2 new avenues. Belated recognition that 2 taxa were involved required concrete resolution of the phylogenetic identity of the *S. altirostris* holotype. Separately, KVR, DFL, and TSS reviewed available vocalizations identified as *S. altirostris*, which revealed an early recording attributable to *S. krabbei* (XC20182, from 1983), and led us to the field experiences of AJS. In brief, AJS performed playback observations between *S. krabbei* and *S. altirostris*, at a time when the vocalizations of the 2 were still confused. Recordings by AJS in 2009 from an unidentified *Scytalopus* at Bosque Unchog provisionally were assigned to *S. altirostris*, as they were similar to DFL's recordings from Cerro Patricia (therefore, these in fact represent *S. krabbei*). Later, in 2012, AJS found that *S. altirostris* at Abra Barro Negro did not respond to playback of his Bosque Unchog recordings, but had a different song; this is not surprising in hindsight, as to date only *S. altirostris* is known from Abra Barro Negro. Furthermore, AJS found that birds at Abra Barro Negro responded strongly to playback of their own songs. On a later (2013) return to Bosque Unchog, AJS encountered the same song type that he had recorded in 2009; playback of recordings of *S. altirostris* from Abra Barro Negro did not elicit a response, but there was an immediate and strong response to playback of his 2009 recordings of *S. krabbei*. Later that same day, at a higher elevation (treeline) at Bosque Unchog, AJS found *S. altirostris*, which did not respond to recordings of the Bosque Unchog *S. krabbei*, but again were responsive to playback of *S. altirostris*. In 2016 at Abra Barro Negro, AJS repeated his playback scheme with the same results. Not surprisingly, he came away from these experiences convinced that multiple species were involved, as confirmed by the genetic analysis. Finally, recordings in 2012 by FA, at new sites in the Cordillera de Colán, match recordings of *S. krabbei*, and confirm that it is widespread in that cordillera. Thus, although there was some evidence all along of the distinctiveness of *S. krabbei*, it was not diagnosed as a separate taxon until recently, in contrast to the history of the following 2 new species detailed below.

Scytalopus frankeae sp. nov.
[K. V. Rosenberg, T. J. Davis, G. H. Rosenberg, P. A. Hosner, M. B. Robbins, T. Valqui, and D. F. Lane]
Jalca Tapaculo

Holotype

LSUMZ 128615; adult male, collected by G. H. Rosenberg (GHR 2267) on July 26, 1985, in Peru: Huánuco: Maria, Millpo, LSU field camp on the trail from Pozuzo to Chaglla, coordinates: 9.894°S, 75.747°W, elevation: 3,675 m. Vocalizations audio recorded by G. H. Rosenberg (ML 195148). Tissue sample LSUMZ B-8343. ZooBank registration 8947DB55-8013-401B-9E39-DEB2E158917B.

Diagnosis

A small *Scytalopus* with a faint to moderately pronounced pale supercilium, a brown rump and lower flanks, and tail with distinct cinnamon bars or vermiculations (Figure 1). Similar to *S. altirostris* from north of the Huallaga Valley in northern Peru and probably not distinguishable from this species based on plumage alone. The bill base of *S. frankeae* averages less deep than *S. altirostris* (Table 3). *Scytalopus affinis* from the west slope of the Andes in northern Peru is paler gray, has little or no white superciliary, and averages slightly longer-billed. *Scytalopus krabbei* is larger, has less bright brown hind-parts than *S. frankeae*, no pale superciliary markings, a less distinctly patterned tail, a narrower bill, and a white patch in the wing. The new species from Ayacucho and Apurímac (described below) is also similar, but it has darker gray upperparts and underparts; and ochraceous flanks with denser and straighter barring. *Scytalopus frankeae* is best distinguished from these and other similar above-treeline forms genetically and vocally, and on the basis of geographic range.

Parapatric *S. acutirostris* is readibly distinguishable from *S. frankeae* by its thinner bill, and by the adult male being entirely blackish gray (the southern population with some dark brown, but no bars on the flanks). Female *S. acutirostris* is paler gray than males and has barred flanks, and thus is superficially more similar to both sexes of *S. frankeae*. However, female *S. acutirostris* lacks the whitish supercilium present in most of *S. frankeae*, has a grayer, unmarked mantle (rather than a light brown or grayish brown mantle scalloped with dusky), and its tail is uniformly dusky rather than light brown and barred with black. *S. frankeae* and *S. acutirostris* also differ in the color of tarsi and toes in live or recently collected birds: in *frankeae,* they range from pale yellowish tan to light vinaceous brown; in *S. acutirostris,* they range from light gray-brown to brownish black.

Description of Holotype

Forecrown, crown, and auriculars dark gray (3/N). Lores gray (5/N). Preocular spot darker gray. Silvery white

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supercilium beginning, narrowly, above the anterior edge of the eye, broadening behind the eye, and extending posteriorly just above the auriculars, although becoming quite narrow again at the posterior end. Nape, mantle, and scapulars dark gray with a wash of dark reddish brown (5YR3/2). Lower back, rump, and upper tail coverts cinnamon brown (7.5YR3/6), each feather with 2 or 3 subterminal blackish curving bars. Outer rectrices dark reddish brown, with narrow, indistinct subterminal cinnamon-brown bars. Central rectrices dusky, with 2 longitudinal, subterminal streaks of umber brown (10YR4/4) that distally curve medially and reach the shaft. Wing coverts dark gray with a wash of dark reddish brown. Primaries and outer secondaries dusky brown (7.5YR2/4). Inner secondaries and tertials cinnamon brown, with 2 concentric, subterminal, blackish streaks, on each web, that curve medially and cross the shaft. Throat and belly light gray (N6), breast slightly darker gray (N5). Lower flanks and under tail coverts tawny brown (10YR5/8), each feather with 2 or 3 subterminal blackish curving bars. Iris light brown. Bill dark gray. Tarsi and toes yellowish tan. Mass 17.5 g. Skull unossified (typical in adult *Scytalopus*). Ten rectrices. Stomach contained insects (saved). Measurements in mm: wing (flat) 56, tail 36.3, tarsus 19.6, bill from fore-edge of operculum 5.9.

Variation among Males

The extent of the white supercilium in adult male specimens is variable; the pattern of the holotype is typical for birds from Huánuco and Pasco. In 3 individuals from Huánuco (LSUMZ 128625, 128623, 128628) and all 5 specimens from Junín, the superciliary is greatly reduced approaching *S. altirostris*. At the other extreme, the forecrown on some Huánuco specimens also is silvery white and forms a continuous band above the bill reminiscent of *S. schulenbergi*. On 2 of the 20 specimens from Huánuco and Pasco and on all 5 specimens from Junín, all rectrices (not just the central pair) are banded cinnamon and dusky, whereas in the rest the rectrices are dusky with lengthwise tawny vermiculations resembling those of *S. altirostris*. No method exists for aging *Scytalopus* once they have molted from juvenile plumage, so it is uncertain whether this variation in tail pattern is age-related or simply represents individual variation.

Description of Female

Adult females of *S. frankeae* are similar to adult males with the most notable difference being overall browner upperparts coloration (Figure 1). The nape and mantle are brownish rather than grayish ranging from cinnamon-brown to olive-brown (10YR4/2). The upper mantle feathers have a subterminal blackish streak along the shaft, and the lower mantle feathers have 2 subterminal blackish bars. The wing coverts are cinnamon-brown with a blackish subterminal bar, and the primaries are cinnamon-brown with the inner primaries having a small cinnamon-brown spot on the tip of each outer web. Four of 8 females from Junín, however, are similar to males in coloration and pattern except that 2 are lighter gray, richer brown, and have more pronounced paler gray tips to the belly feathers.

Description of Juvenile

No *S. frankeae* specimen is in full juvenile plumage. A few specimens (both male and female) retain portions of juvenile plumage in that the belly is buff (2.5Y8/4) with indistinct dusky bars rather than uniform gray.

Vocalizations

As in many other high-elevation species in *S.* [*magellanicus*], the primary song of *S. frankeae* is a long series of regularly repeated reverberating churrs in bouts lasting several minutes. Its churrs are simple, without the distinct introductory stroke of its sister species *S. altirostris*, and are composed of fewer (2.6 ± 0.3) and slower-paced (30 ± 3) strokes (no overlap) (Table 1; Figure S1). The frequency range of its churrs are greater than in any other species in the *S.* [*magellanicus*] complex (Figure 4). The pace of its churrs in natural song is among the slowest of the species in the complex, but is decidedly faster in response to playback (see note under Table 1). There are slight differences between churrs of birds from the northern end of the range (Huánuco) and those from Junín. In northern birds (n = 7; Figure 4D, panels 1–4), the first stroke is usually somewhat louder than the remainder and begins with an upstroke. In southern birds (n = 25) (Figure 4D, panels 5–8), churrs lack the loud first upstroke and are thus on average half a stroke shorter (Table 1). Only 2 types of calls have been recorded. One call given by a female in Huánuco (Figure 5C, panel 1) is a single note repeated at a pace similar to that of churrs in the male song, but more widely and irregularly spaced. The other call, recorded in Junín (n = 4), is a single churr given at 2 to 6 s intervals, presumably by males (Figure 5C, panels 2–3), and may be remarkably similar to the churrs in song of *S. altirostris* (compare Figures 4C, panel 2 and 5C, panel 3).

Scytalopus frankeae song has been previously described and illustrated (as an unnamed taxon) on pages 440–441 in Fjeldså and Krabbe (1990), figure 4B in Whitney (1994), and figure 34 in Krabbe and Schulenberg (1997). Zimmer (1939) also described similar vocalizations from birds at their "Huánuco Mts" collecting site: the only note heard was a rather slowly repeated, "tyoók, tyoók, tyoók…." Song of the parapatric *S. acutirostris* is different, consisting of an introductory note followed by a short or long rough trill (see figures 44–46 of Krabbe and Schulenberg 1997).

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Distribution

Scytalopus frankeae is known from 2 geographically separate populations. The northern population is known from 3 areas in Huánuco and Pasco: the type locality above Millpo, Huánuco (occasionally spelled Milpo; originally thought to be located in Pasco and near the border between the 2 departments; 9.894°S, 75.747°W); Pagancho, Huánuco ("Huánuco Mts."; presumed to be in the vicinity of Laguna Parguincha: 9.968°S, 76.131°W) and above Schismay (also in "Huánuco Mountains;" approximately 9.971°S, 76.166°W); and, Chipa, Pasco (approximately 10.7°S, 75.9°W). The southern population is found in Junín at the following known localities: Maraynioc (approximately 11.35°S, 75.45°W), Río Satipo near Toldopampa (11.487°S, 74.886°W to 11.531°S, 74.943°W), Apaya-Andamarca road (11.545°S, 74.811°W), Runatullo (11.646°S, 74.960°W), 12.8 km after the fork to Acobamba (11.673°S, 74.881°W), and Chilifruta (also known as "approximately 5 km WSW of Lampa"; 11.990°S, 74.935°W). The northern limit of the species' distribution coincides with the Río Huallaga, north of which *S. altirostris* replaces *S. frankeae* at similar elevations. The southern limit coincides with Río Mantaro, south of which *S. frankeae* is replaced at similar elevations by the new species from Ayacucho and Apurímac described below. *S. frankeae* is recorded at elevations of 3,400–4,200 m and replaced at lower elevations and in adjacent forest and shrubbery by *S. acutirostris*.

Habitat

The natural habitat transition between the cloud-forest zone and the barren zone above treeline in much of the Andes is now heavily reduced because of intensive human use of fire to manage pastures (e.g., Lægaard 1992, Kessler and Herzog 1998). Several *S.* [*magellanicus*] species are therefore often restricted to remaining patches of elfin forest or rocky terrain or boulder scree with low scrubs or tall bunchgrass (mostly *Festuca*) in the otherwise heavily disturbed bunchgrass zone. The type locality of *S. frankeae* is on the uppermost slopes of a semi-isolated spur of the humid eastern Andes above stunted treeline forest 5–9 m tall; actual treeline varied from 3,600 to 3,850 m, with scattered patches of trees in sheltered ravines to 3,900 m. Above treeline, where *S. frankeae* was common, dense bunchgrass (*Festuca*) and scattered shrubs occurred on steep rocky slopes; flatter areas were heavily grazed by cattle and sheep and were strewn with boulders. Human disturbance was extensive above 3,500 m with several houses in large clearings and a few small planted plots. Individual *S. frankeae* were associated almost exclusively with steep rocky slopes above treeline with dense bunchgrass or shrubs. Males often sang from exposed rocky outcrops on nearly vertical slopes. Two individuals were in grazed grassy areas near human habitations, and 3 were recorded at the edge of stunted, treeline forest. In Junín, near Toldopampa, habitat associations were similar. *Scytalopus frankeae* inhabited scattered shrubs including isolated *Gynoxys* patches 3,600–3,800. Higher in elevation, where no shrubs were present, *S. frankeae* inhabited ravines with bunchgrass as the only structural vegetation. The species has also been recorded in *Polylepis* (XC82631), and "riparian evergreen forest" (ML82833). By contrast, all records of *S. acutirostris* from the same localities were associated with closed montane forest, often in dense bamboo understory. The uppermost individuals were often in patches of forest that followed ravines up the slopes above the surrounding treeline. The 2 species overlapped considerably in elevational range and could be observed in adjoining territories, but habitat segregation was nearly complete. Co-occurrence was in the form of interdigitating forest patches and grassland at treeline, with only the smallest, highest, and most isolated forest patches inhabited by *S. frankeae*.

Life History and Behavior

Scytalopus frankeae was vocal at Millpo in late July–early August 1985, suggesting territorial behavior and breeding. The species was frequently encountered in close pairs, often with both members of the pair vocalizing. The series of specimens also indicates breeding activity, with at least half of the males exhibiting enlarged testes (at least 5 × 3 mm; up to 9 × 5.5 mm) and all 4 females showing enlarged ovaries (5 × 3 mm to 8 × 3 mm). Nine specimens exhibited no molt, 8 showed trace or light molt, and 2 were in moderate molt. Evidence from a wide range of species at this elevation indicated that our survey coincided with the end of the breeding season for most of this bird community. The parapatric *S. acutirostris* was also quite vocal with a majority of specimens exhibiting enlarged gonads. Observations indicate that the behavior of *S. frankeae* is similar to that described for other *S.* [*magellanicus*]. One was seen hopping near the ground along the mossy bases of stunted trees. A female was observed "scurrying along the top of a gully at the base of some shrubs, running over moss-covered rocks and seeming to disappear through tunnels in the overhanging bank" (K. V. Rosenberg personal observation). At Toldopampa, Junín, birds were in breeding condition in late September (ovaries 8 × 3 mm, 7 × 5 mm, 4 × 3 mm, testes 6 × 3 mm), and specimens were in heavy molt.

Conservation

Although *S. frankeae* was common at the type locality, and seemed to occur in high densities in appropriate habitat on steep rocky slopes, the total extent of potential habitat at appropriate elevation within the Huánuco portion of the distribution is small: only ~1,400 km^2. A large portion of this potential habitat is highly disturbed, especially in the drier Huánuco Mountains, where Zimmer collected

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his specimens in 1922. Nearly every accessible part of this region, south to the Chipa, Pasco location, has been heavily grazed and burned to manage pastures, and suitable bunchgrass habitat likely occurs today only on the steepest rocky slopes and cliffs. In addition, no protected areas exist within its range in this region. The same applies for parts of Junín, but the southern population of the species occurs in a much larger and less populated area, which almost certainly includes the higher parts of the protected area Bosque de Protección de Pui-Pui (600 km^2). They appear to be common throughout the Toldopampa valley. For this reason, we recommend that, overall, *S. frankeae* be categorized as a species of LC in the IUCN Red List of Threatened Species (IUCN 2019).

Etymology

We are pleased to name this new tapaculo in honor of Dr. Irma Franke, our friend, colleague, former curator of the bird collection at the MUSM, and a major contributor to Peruvian ornithology for over 30 yr. It is especially fitting to name this taxon after her because she participated in the Millpo expedition that discovered the bird in 1985. The recommended English name uses a local Peruvian term for puna and páramo habitat ("jalca") that has tussock grasses as a primary component, which was the habitat primarily used by the species at the type locality (although less so in Junín). Colloquially, this species has been called Millpo Tapaculo. However, we consider this name to be inappropriate, primarily because Millpo is now known to be at the geographic periphery of the range of the species. Our proposed English name is more reflective of the habitat of *S. frankeae* throughout its distribution.

Remarks

Scytalopus frankeae is exceedingly similar in appearance to its sister taxon, *S. altirostris*, but clearly can be considered a phylogenetic species on the basis of its genetic divergence (Criterion 3) and diagnostic vocal characters (Criterion 2). Application of the biological species concept is less straightforward, as *S. frankeae* is allopatric to *S. altirostris*, and indeed to all other members of the *S.* [*magellanicus*] complex. Geographically, the distributions of *S. frankeae* and *S. altirostris* approach one another closely, although they remain separated by the low arid canyon of the upper Huallaga River. The fact that the songs of these tapaculos changes sharply across this geographic barrier is consistent with the idea that no gene flow unites their populations, and the best evidence that *S. frankeae* and *S. altirostris* are reproductively isolated as well.

Vocalizations, one plumage character, and ND2 sequences all show geographic variation within *S. frankeae.* Sampling is geographically biased, with most specimens and audio recordings from either the far northern or southern end of its distribution. ND2 sequences from Huánuco and Junín differ by 2.9–3.0% (uncorrected pairwise divergence). Because of this sampling bias, it is difficult to ascertain if variation is gradual or clinal, or whether *S. frankeae* is composed of 2 differentiated populations. If the latter, the Junín population could warrant naming, and northern *S. frankeae* would occupy a much smaller distribution. We recommend that future survey efforts focus on the seldom visited but easily accessible near-treeline sites in Pasco and northern Junín, which should hold this species. The southernmost records of *S. frankeae* are near the Huancavelica border, and we expect that exploration in Huancavelica north of the Río Mantaro will confirm its presence there.

Both Hellmayr (Cory and Hellmayr 1924) and Zimmer (1939) applied the name *S. acutirostris* (Tschudi 1844) to birds now referred to as *S. frankeae* and *S. simonsi*. This was followed by both Peters (1951) and Whitney (1994). We have examined the type specimen of *S. acutirostris* and are convinced that it does not represent any member of *S.* [*magellanicus*]. It might represent either of 2 species found at lower elevations than *S. frankeae*, but for now we follow Krabbe and Schulenberg (1997) in the usage of the name. Persistent confusion in the application of these names, however, was partly responsible for the long delay in resolving species limits and describing *S. frankeae*. At the time of our 1985 expedition to Millpo, for example, the all-dark tapaculo abundant in treeline forest was believed to represent *S.* [*magellanicus*]. We were therefore surprised to discover the new pale-browed taxon above treeline and made a particular effort to document its distribution with additional specimens (including tissues) and sound-recordings. The dark treeline birds are now considered to represent *S. acutirostris*, and the previously unnamed *S. frankeae* has proven to be representative of the true high-elevation *S.* [*magellanicus*] clade, and includes the specimens originally collected by Zimmer (1939) in the nearby Huánuco Mountains.

Scytalopus whitneyi sp. nov.
[N. K. Krabbe, J. Fjeldså, P. A. Hosner, M. B. Robbins, and M. J. Andersen]
Ampay Tapaculo

Holotype

NHMD 80025; adult male, collected by N. K. Krabbe and J. Fjeldså (NK1-18.3.87) on March 18, 1987, in Peru: depto. Apurímac: mountains north-northeast of Abancay: Cerro Turronmocco, coordinates: 13.518°S, 72.888°W, elevation: 3,500 m. Vocalizations audio recorded by N. K. Krabbe (ML230279/XC436055, XC436056, XC436057). Tissue sample preserved (ZMUC tissue-125144). ZooBank registration C504C4E5-38A0-4DEA-BD4E-C54C68C53984; ND2 sequence GenBank MN692540.

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Diagnosis

A small *Scytalopus* resembling other central and southern Peruvian members of *S.* [*magellanicus*] by the presence of a pale superciliary, which varies considerably in extent. In some individuals it is barely suggested, whereas in others it is more pronounced or even joined across the forecrown with a silvery sheen contrasting with the black lower forehead and lores (Figure 1). *Scytalopus whitneyi* is readily distinguished from *S. frankeae*, *S. urubambae*, and *S. simonsi* by its overall darker gray plumage and its duller and darker ochraceous brown flanks, rump, and vent, with relatively dense, narrow, and straight barring. The dark brown tail is scribbled with longitudinal markings like some individuals of *S. frankeae*. In *S. urubambae* and *S. simonsi*, the tail is dark brown and variably uniform, barred, or with scribbled markings. *Scytalopus whitneyi* can be similar to *S. schulenbergi* in its head markings, but *S. schulenbergi* has a uniform blackish tail, a slightly heavier bill, and light brown flanks with coarse and sparse barring (Cusco) or unbarred dark flanks (Puno, Bolivia).

Description of Holotype

Above dark fuscous (2.5Y/R2.5/1). Lores and ocular region black (N2.5). Crown with a light gray (N7) sheen when seen head on, most noticeable above eye, forming a faint eyebrow. Tips of secondaries, bars on lower back and rump, edges all around on rectrices and presubterminally on the tip of each rectrix strong brown to ochraceous tawny (7.5YR4/6–10YR4/6). Underparts gray to dark gray (5Y5/1–4/1), throat with slightly paler sheen. Flanks and under tail coverts with numerous straight, ochraceous tawny (10YR4/6) and dusky (7.5R2.5/1) bars. Rectrices dusky with faint longitudinal dark yellowish brown (10YR4/6) markings. Ten rectrices. Mass 14.7 g. Iris dark brown, bill blackish, feet dark brown. Skull unossified. Wing-, tail-, and body-molt. Testes 1 mm. Stomach contained insects. Measurements (mm): wing (flat) 54.5, tail 39, tarsus 20.5, bill from fore edge of operculum 5.6 mm.

Variation among Males

An adult male (NMHD 80110) is similar to the holotype, but the pale supercilium is more pronounced. Another adult male (LSUMZ 179689) is virtually identical to NHMD 80110, but its forehead is paler, in some lights forming a band across the forehead reminiscent of *S. schulenbergi*. A third male (MSB 33916) matches the type. The 3 males from Ayacucho have weakly developed superciliaries and lack the contrasting blackish lores and ocular region seen in the Apurímac specimens. All 3 had enlarged testes and a variable brownish wash to the mantle, suggesting they were subadults. Also, the fact that the Ayacucho female had a more strongly developed superciliary (see below) suggests that these plumage differences from Apurímac birds are age-related and not geographic.

Description of Female

The single known female specimen (KU 122548) is from Ayacucho. Unlike male specimens from Ayacucho it has a narrow but prominent pale supercilium, widest over the eye. Throat and breast lighter gray (5/N) than in males, and the nape and back are slightly browner. Most of the upperparts are dark reddish brown (5YR3/3), wings, central and lower back, rump, and upper tail coverts barred blackish. The lower underparts are buffy brown (7.5YR5/3), sides, flanks, and vent narrowly and densely barred black as in males. The longitudinal markings on the tail resemble those found in males, but are more pronounced.

Vocalizations

Primary song ($n = 24$) differs from all other *S.* [*magellanicus*] by consisting of a single repeated note (Figure 4E, panels 1–4). The secondary song ($n = 9$) is composed of regularly repeated churrs (Figure 4F, panels 1–5). The pace of strokes in the churr is faster than in both populations of *S. frankeae*, without overlap (Table 1), but slower than in *S. urubambae*, without overlap. Call (scold, only recorded from Apurímac; $n = 4$) 0.2 or 0.5–0.6 s long, composed of 2 or 3 similar, rising notes, first or second harmonic variably loudest, second harmonic loudest at 3.0–3.7 kHz (Figure 5D, panels 1–2). There is some indication that Ayacucho birds differ slightly vocally from Apurímac birds, the primary song ($n = 6$; Figure 4E, panels 3–4) being on average higher pitched, and the only example of secondary song ($n = 1$; Figure 4F, panel 1) having a slower pace of strokes (Table 1).

Distribution

Scytalopus whitneyi is known from 2 geographically separate populations. One population is in eastern Ayacucho south of Río Mantaro and is known from: Huisca (12.832°S, 73.923°W), 9.5 km SE Pacobamba near Anco (13.099°S, 73.693°W), 5.0 km NW Chungui (13.186°S, 73.651°W), Chupón (13.243°S, 73.514°W), and Yanacocha (13.255°S, 73.522°W). The other population occurs in Apurímac between the Río Apurímac and Río Pampas and is known from the following localities, all within 26 km of Abancay: Ccocha (13.484°S, 72.982°W), near Huanipaca road (13.500°S, 72.932°W), Cerro Turronmocco (type locality, also referred to as Huanipaca road) (13.518°S, 72.888°W), almost throughout Bosque de Ampay including at Laguna Angascocha (13.593°S, 72.881°W), Las Cuevas (13.586°S, 72.886°W), and 7 km N Abancay (13.570°S, 72.886°W), near the pass on the main road above Abancay (13.583°S, 72.838°W), 2 forests on Cerro Queñua Khasa near Runtacocha (13.6775°S, 72.7929°W and 13.6768°S, 72.7826°W), Quebrada Balcón (13.7033°S, 72.7058°W), and at 2 sites in Quebrada Chua: on the south slope of Cerro Casiniso (13.7635°S, 72.6836°W) and at Laguna Pumacocha (13.7538°S, 72.6782°W). Apparently absent

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further south in Apurímac, as it was found to be absent from *Polylepis* forests at 4,360 m near Laguna Antanay despite targeted searching (14.061°S, 73.001°W; Benham et al. 2011). It might also occur in some of the many unexplored patches of seemingly suitable habitat between Río Chalhuanca and Río Pampas. Recorded at elevations of 3,500–4,200 m in Ayacucho, 3,150–4,500 m in Apurímac. In Ayacucho, it is replaced in forest below by *S. parvirostris*; in Apurímac, where humid forest is largely confined to the highlands, no other *Scytalopus* is known.

Habitat

Common in montane forest and shrubbery in Apurímac (Fjeldså and Krabbe 1990, Baldwin and Drucker 2016); its highest population density seems to be in closed, mossy *Podocarpus* forest, but in Bosque Ampay it is also common in *Escallonia* and areas with dense thickets of *Berberis*, *Barnadesia,* and *Hesperomeles*. The Bosque Ampay population is distributed at 3,150–4,000 m. In the highlands south-east of Abancay, the species strangely appears to be almost completely restricted to patches of closed *Polylepis incana* forest at 4,080–4,500 m and absent from mixed forest habitats (*Eugenia*, *Polylepis weberbaueri*, a few *Podocarpus* trees, and various dense scrubs) below 4,000 m. In Ayacucho it appeared to be excluded from forested areas by *S. parvirostris*, and it was instead found in open shrubby (*Baccharis*) and bunchgrass (*Festuca*) habitats. These non-forested areas were heavily disturbed by grazing and burning, and *Scytalopus whitneyi* was generally restricted to steep rocky slopes inaccessible to fire and cattle. It was also found in a single small patch of *Gynoxys* woodland isolated from continuous forest (Hosner et al. 2015).

Life History and Behavior

Behaves much like other highland *Scytalopus* tapaculos. Tunnels through moss, roots, rocks, and bunchgrass, and hops along trunks and across twigs and branches near the ground in pursuit of small arthropods. *S. whitneyi* was found to stay on its territory in the cavities among boulders when the area was covered (for a single day) by snow, even singing from below the snow (Fjeldså 1991). During territorial disputes or moments of little disturbance, it would perch conspicuously atop a rock or vegetation for brief periods while singing. The single known nest was an open cup placed in a rock crevice, and, as typical of the genus (Greeney 2008), the brood size was 2 (Baldwin and Drucker 2016). Stomach contents were insect remains in 3 specimens (2 stomachs saved), in a fourth "small worm, brown mush, several 1 × 1 mm gnats".

Conservation

Scytalopus whitneyi is fairly common in Apurímac, generally with 100–200 m between territories in Bosque Ampay, but outside this large forest tract its habitat is patchy and threatened by grazing and burning, thus leaving the species vulnerable. The species is widespread within Santuario Nacional de Ampay (Bosque Ampay), a 36.4 km^2 large area declared a wildlife sanctuary in 1987, about half of which is forested. Unless heavy deforestation or natural disaster occurs, the population in Bosque Ampay should be viable (based on observed density we estimate 450–1,800 pairs). In Ayacucho the species is local, uncommon, and restricted to ravines and steep slopes less affected by burning and intense grazing pressure. Apart from Bosque Ampay, *S. whitneyi* receives no legal protection. Some local communities appear to be conscious of the importance of maintaining woodland patches to ensure access to native plant resources and a steady water supply, but the practice of burning for fresh pasture and cutting for firewood persists in many areas. On present knowledge, population size, distributional range, and known decline do not fulfil the criteria for considering the species as threatened, but due to the threats and vulnerabilities mentioned, we recommend that *S. whitneyi* be categorized as near-threatened in the IUCN Red List of Threatened Species (IUCN 2019).

Etymology

We take the opportunity to honor our friend and colleague Bret M. Whitney for his outstanding contributions to Neotropical ornithology over the past 3 decades. Bret's keen eyes and ears, and his insightful attention to vocalizations and natural history, have given us a much greater understanding of variation and species limits in several challenging groups of tropical birds, and particularly in *Scytalopus*. The recommended English name refers to Bosque Ampay, the only protected area where the species occurs.

Remarks

Scytalopus whitneyi is allopatric with all other members of the *S.* [*magellanicus*] complex, as typical of most members of this clade. Its distribution does closely approach that of *S. urubambae* (Criterion 1), which, however, differs from *S. whitneyi* by having a generally pale gray plumage and bright, unbarred cinnamon-rufous flanks (Criterion 4). *Scytalopus whitneyi* is genetically divergent from all other members of the complex (Criterion 3), and has a distinctive song type not expressed in other *S.* [*magellanicus*] (Criterion 2). Based on these consistent differences, *S. whitneyi* is clearly a distinctive evolutionary lineage. Given that these differences have been maintained in narrow allopatry with other *S.* [*magellanicus*], we hypothesize that *S. whitneyi* would be reproductively isolated from *S. frankeae* and *S. urubambae*.

Populations in Apurímac and Ayacucho differ subtly in plumage and vocalizations. However, these differences are difficult to interpret because of small sample sizes of audio recordings and specimens. The 2 populations differ

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by 1.2–1.4% in ND2 sequences (uncorrected pairwise divergence). This species could also occur in a limited area of treeline forest that occurs south of the Río Mantaro on the east slope in Huancavelica, adjacent to Ayacucho.

Vocal Diagnosis and Geographic Variation of Other Peruvian *Scytalopus* [*Magellanicus*]

For comparison with the new taxa described above, we provide detailed descriptions of the vocalizations of additional species in *S.* [*magellanicus*] as an update to Krabbe and Schulenberg (1997, 2003). We also discuss geographic variation in plumage and genetic variation, where it occurs. Details on vocalizations of the 3 northern forms (*S. canus*, *S. opacus*, and *S. o. androstictus*) were reviewed and described by Krabbe and Cadena (2010). Note that under the species concept and operational criteria presented here (see Taxonomy), *S. o. androstictus* fulfills both criteria 2 and 3, and consequently should be ranked as a species.

Scytalopus affinis: song (n = 18) usually of fixed length, 5–16 s long, a series of repeated churrs given at a pace of ~3 s^{-1}, faster than in *S. altirostris*, *S. frankeae*, *S. whitneyi*, *S. urubambae,* and *S. simonsi*, but slower than in *S. krabbei*. The pace often accelerates slightly towards the end of the song and occasionally at the beginning. The churrs may be of similar pitch through the song, but more often the pitch rises about half an octave, most of which is during the first quarter of the song. The pace of strokes in each churr averages faster than in other species overlapping only with *altirostris*, in which churrs begin with a loud first harmonic, and with *urubambae*, which is lower pitched overall. The average pitch through each churr may be level, descending, or rising, and also varies in frequency amplitude (Figure 4A, panels 1–5). The scolding call (Figure 5A; n = 9) given by both sexes is a short, dry trill composed of steep unmodulated downstroke notes only, similar to scolds of *Myornis senilis* and to scolds of Peruvian populations of *Scytalopus parvirostris*. Scolds are 0.7 (0.6–0.9) s long, composed of 13–18 regularly repeated similar notes given at a pace of 19–21 s^{-1} with the loudest pitch at 3.2–4.0 kHz (Ancash, n = 8). In a single recording from Lima, the scold is longer (1.2 s), of more notes (19), slower paced (15 s^{-1}), and at lower pitch (3.1 kHz). No other geographic variation in vocalizations is evident. By comparison, the scold of *S. androstictus* is higher pitched, and each note is an up-down stroke with a loud and long peak frequency; the scold of *S. krabbei* is of different quality with modulated notes and decidedly slower paced.

Scytalopus altirostris: churrs of the previously undescribed song (n = 10; Figure 4C, panels 1–6) begin with a long loud note that usually falls by about an octave and usually has most volume on the first harmonic, but in one recording (XC40729), the first note has a smaller frequency range and most volume is on the second harmonic, thus being remarkably similar to some single churrs given by *S. frankeae*. In all churrs, the following strokes are connected and fairly similar to each other, have loudest second harmonic (as most other *Scytalopus* songs), and are variably rising, level, or falling in average pitch. The pace of strokes in the churr is relatively fast, on average faster than in *S. urubambae* and slower than in *S. affinis*, but overlapping with both. No calls have been recorded. No geographic variation is evident.

Scytalopus urubambae: song (n = 12; Figure 4G, panels 1–4) of regularly repeated churrs, pace of strokes in churr faster than in *S. whitneyi*. During bouts of counter-singing, a male may momentarily intersperse song with high-pitched (6.5–5 kHz) descending series of churred notes ("frustration call"). Call (scold; n = 10) by female and probably also male, a 0.6–1.0 s long series of 5–7 churred notes similar to the churrs in the song in pace of strokes, but shorter and higher pitched (3.45–3.8 kHz; Figure 5E). There is no geographic variation within its restricted distribution.

Scytalopus simonsi: each churr in the song (n = 14 from Cusco, 6 from Puno and northern La Paz) begins with a separate, loud, long, and distinctive note (Figure 4H, panels 1–5). The rest of the churr is uniform but varies in average length, number of strokes, and in pitch, which in Peru and northern La Paz may be level or rising, but usually not falling. Call (scold; n = 8) 0.5–1 s long, a series of 6–12 notes at 3.3–3.9 kHz given at a pace of 9–12 s^{-1} (Figure 5F). Scolds of *S. schulenbergi* from Cusco and northern La Paz (n = 9) are similar but on average longer (0.7–1.3 s), with more notes (9–18) given at a faster pace (11–15 s^{-1}) and also on average lower-pitched (3.0–3.5 kHz). No geographic plumage variation is evident, but ND2 sequences of Cusco and Puno specimens differ by 2.3–2.8% (uncorrected pairwise divergence).

Scytalopus schulenbergi: vocalizations were described by Whitney (1994). Despite their similar voice, populations from Cusco and Puno differ from each other by 3.1%, those from Cusco and La Paz by 3.7%, and those from Puno and La Paz by 2.4% in ND2 sequences (uncorrected pairwise divergence; Figure 6). Cusco populations also appear unique in having contrasting brown rather than uniform dark gray flanks. Deeper sampling of genetic markers is needed to resolve the *S. schulenbergi* (Puno/La Paz), *S. schulenbergi* (Cusco), *S. urubambae*, and *S. whitneyi* polytomy.

DISCUSSION

Our results demonstrate that field exploration and careful attention to natural history and behavior continue to identify cryptic new species of birds, particularly in complex tropical environs, such as the Peruvian Andes. We employed an integrated framework made possible by a combination of vocal information, mitochondrial DNA sequences, and plumage characters, gathered from our own fieldwork over the past 40 yr and supplemented with community-shared

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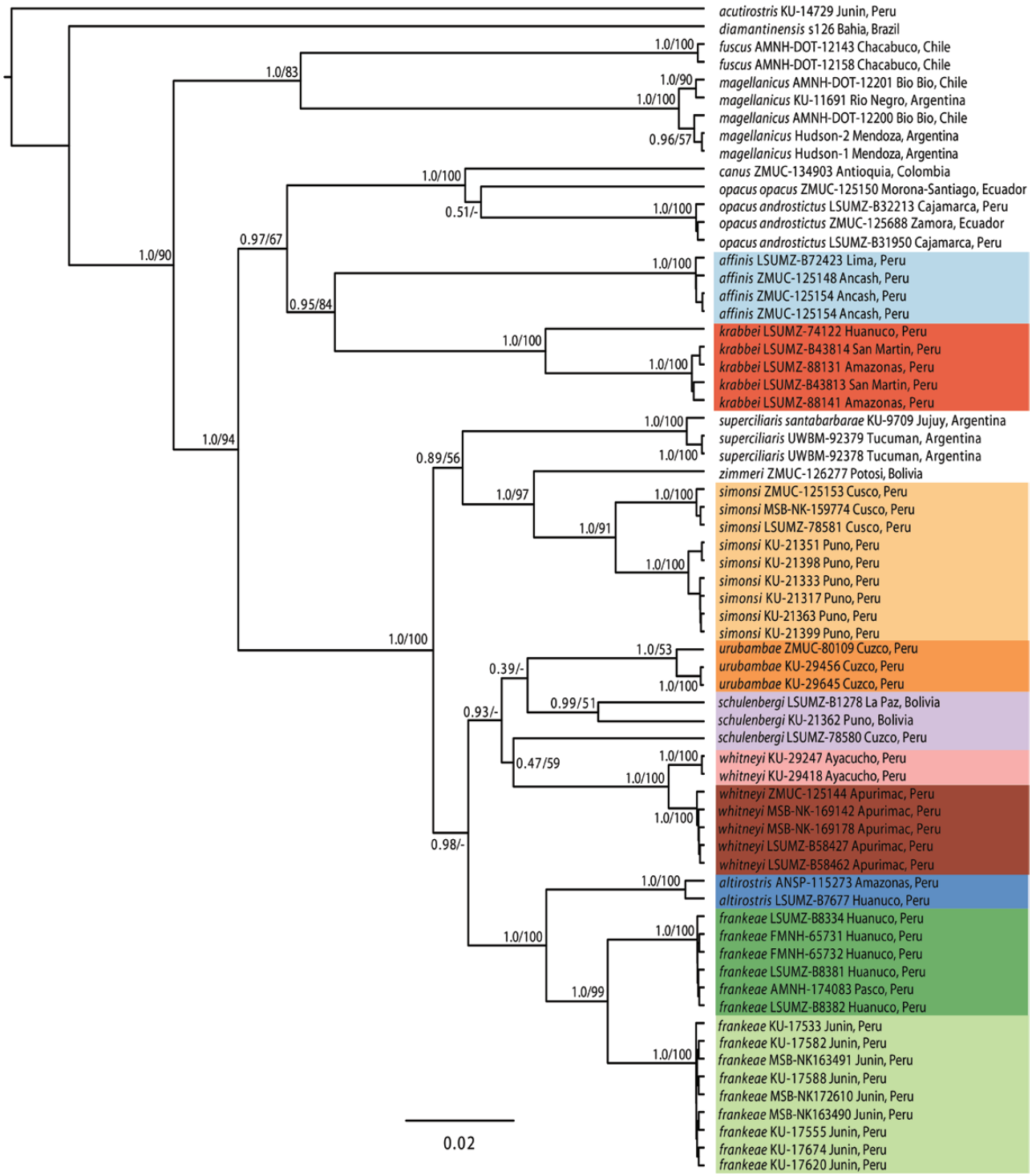

FIGURE 6. *Scytalopus* [*magellanicus*] ND2 mitochondrial genealogy inferred with BEAST. Node support values are BEAST posterior probabilities followed by RAxML maximum likelihood bootstrap values. Color highlighted selected populations correspond to those used in Appendix Figure 7. Although the 3 newly described species, *S. krabbei*, *S. frankeae*, and *S. whitneyi*, together form a nearly continuous distribution and replace each other geographically from Amazonas to Apurímac, they are not sister taxa, each being related to another nearby *S.* [*magellanicus*] taxon.

birdsong archives and museum specimens. The existence of at least 2 unnamed Peruvian tapaculos in the *S.* [*magellanicus*] complex has been known for many years (Fjeldså and Krabbe 1990, Schulenberg et al. 2010), but until now the affinities of these taxa had remained elusive, preventing formal description. The presence of a third new

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species "hiding in plain sight" in the northern Peruvian Andes was more surprising, however. In addition to these newly described species, application of our species recognition criteria also results in the elevation of an extralimital taxon from subspecies to species, *S. androstictus* of southern Ecuador and northernmost Peru. Our approach has significantly increased the known diversity within the already species-rich genus *Scytalopus*. When applied more broadly throughout the genus, we expect these criteria will diagnose additional cryptic species awaiting discovery.

Complex topography is coincident with *S.* [*magellanicus*] species turnover across the high Andes of Peru. The Huancabamba, Marañón, Huallaga, Mantaro, Pampas, Apurímac, and Urubamba river valleys all bound the distributions of populations, as identified by vocal groupings and mtDNA sequences. However, 2 pairs of Peruvian S. [*magellanicus*] species have parapatric distributions, which could imply a role for diversification along elevation gradients. However, little evidence supports that populations evolved through parapatric speciation, because species replacing each other elevationally are not sister taxa (Patton and Smith 1992, Moritz et al. 2000, Cadena and Céspedes 2020). *Scytalopus krabbei* is sister to *S. affinis*, a species isolated across the deep Marañón Valley, rather than to *S. altirostris* with which it co-occurs. *Scytalopus schulenbergi* in turn is a close relative of *S. urubambae* and *S. whitneyi*, which could be considered geographical replacements across the Urubamba and Apurímac rivers, respectively. *Scytalopus schulenbergi* is not a close relative of *S. simonsi*, with which it is parapatric. Hence, isolation of populations across strong geographic barriers appears to be the primary driver of diversification in high Andean tapaculos.

Rather than reflecting ecological speciation, parapatric distributions of *S.* [*magellanicus*] must instead be the result of species assembly along elevational gradients, with multiple species from independent source populations occurring in geographical proximity (Patton and Smith 1992, Moritz et al. 2000, Cadena and Céspedes 2020). The discovery of *S. krabbei* demonstrates that 6 *Scytalopus* species replace each other elevationally along the Amazonian slope in north-central Peru, from southern Amazonas to northern Huánuco. This diversity of congeners along an elevational gradient in birds is matched only by *Scytalopus* in the Río Satipo Valley in Junín (Hosner et al. 2013, XC229596).

Evidence from field observations of *S.* [*magellanicus*] in Peru suggests that at least some *Scytalopus* populations are flexible in their habitat preferences, and that realized elevational distributions may depend strongly on the presence or absence of other co-habiting species. Habitat occupation by *Scytalopus krabbei* appears to vary markedly depending on which other *Scytalopus* species are found along the same elevation gradient. At Cordillera Colán in northern Amazonas, where *S. altirostris* is absent, *S. krabbei* is common at treeline, and *S. acutirostris* inhabits closed-canopy forest. At Cerro Patricia in San Martín, where both *S. altirostris* and *S. acutirostris* are absent, *S. krabbei* occupies treeline scrub and closed-canopy forested habitats. However, at Bosque Unchog, Huánuco, where all 3 species co-occur, *S. acutirostris* occupies closed-canopy forest, whereas *S. krabbei* and *S. altirostris* occupy transitional elfin forest habitats and shrubby open puna habitats. Partitioning between *S. krabbei* and *S. altirostris* at Bosque Unchog remains poorly understood. Competitive exclusion or habitat partitioning could also explain why *S. krabbei* is rare, local, or underreported throughout its distribution, being hard pressed for space by interactions with other *Scytalopus* species (Remsen and Graves 1995, Jankowski et al. 2010).

Similarly, *S. whitneyi* has a broad elevational distribution and generalist habitats in Apurímac, where it is the only tapaculo. There, it occupies closed-canopy forest, elfin forest patches and transitional vegetation, shrubby puna, and *Polylepis/Gynoxys* woodlands. In Ayacucho, *S. whitneyi* is limited to shrubby puna and to isolated patches of *Gynoxys* woodlands, whereas *S. parvirostris* inhabits closed-canopy forests up to treeline. These observations imply either niche partitioning and ecological release mediated by species interactions, or perhaps local adaptations to different environments in different parts of their distributions.

The idea that *Scytalopus* vocal divergence is correlated with genetic divergence has held since the onset of genetic studies of these birds (Arctander and Fjeldså 1994), and broadly, it holds true in *S.* [*magellanicus*] (Cadena et al. 2020). However, at finer scales, we identified several populations that are genetically divergent without perceivable differences in vocalizations. ND2 sequences of *S. krabbei* from San Martín and Huánuco were 4.3–4.4% divergent, more so than many recognized species in *S.* [*magellanicus*], for example, *S. altirostris/frankeae* (3.8–3.9%), S. *urubambae/schulenbergi* (3.4–3.9%), and *S. simonsi/zimmeri* (4.0%). Similarly, *S. schulenbergi* has a strong genetic structure with a morphologically distinct population in Cusco, and a fairly strong structure between Puno and nearby La Paz, Bolivia. *Scytalopus simonsi* also exhibits strong genetic divergence between Cusco and Puno, but without obvious phenotypic differences. In all of these examples, genetic divergence exceeds that found in reproductively isolated tapaculos found on the same slopes (*S. femoralis/gettyae/acutirostris*) that differ only by 2.0% in ND2 (pairwise uncorrected difference; Cadena et al. 2020).

The causes and significance of this genetic structure are uncertain and require further study. The structure could be an example of cryptic differentiation (Bickford et al. 2007), where populations have attained substantial genetic divergence despite morphological and vocal similarity/stasis,

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rendering unique populations unidentifiable without the aid of genotyping. Alternatively, genetic structure could reflect past history, such as signatures of once isolated populations that have since merged, resulting in strong mitochondrial structure in populations without nuclear differentiation (Block et al. 2015, Kearns et al. 2018). To date, geographic sampling within *Scytalopus* species has been limited. Well-sampled phylogeographic studies are needed to complement the existing species-level, phylogenetic framework and to demystify the apparent cryptic diversity within *Scytalopus* and other diverse tropical genera.

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Ethics statement: The study has followed the Commission on Publication Ethics (COPE) guidelines.

Author contributions: The paper was first conceived separately by GRR/KVR/TJD and JF/NKK in the 1980s, after their initial field discoveries of new taxa. As additional data were collected, the idea expanded to combine these descriptions into a single collaborate paper. All authors, except CDC and JFS, took part in the fieldwork. Specimens were obtained by DFL, GRR, JF, KVR, MBR, NKK, PAH, TJD, and TSS, voice recordings by AJS, DFL, FA, GRR, JF, MBR, MJA, NKK, PAH, and TSS. Most DNA sequences were obtained by CDC, some by PAH and JFS. Visual comparisons and assessments were primarily made by NKK and TSS. Most measurements (length of bill, wing, tail, and tarsus) were taken by NKK. DFL took additional measurements (bill depth) from many of the same specimens as well as from some material in AMNH and USNM. A few specimens were measured at KU and CORBIDI by MBR and PAH. NKK, PAH, KVR, and TSS were principal authors and editors, but all authors contributed to and approved the final draft. The Spanish summary was mainly written by TV, who also examined *Scytalopus* specimens in MUSM. NKK analyzed the vocal and mensural data and prepared the sonograms and, with the help of FA, the distribution map. PAH produced PC and phylogenetic analyses and associated figures.

Data deposits: Specimens are preserved in public museums and sound recordings in public libraries as indicated in the Appendices. GenBank accession numbers for sequences used can be found in the text.

Nomenclature statement: The nomenclature in this paper has been reviewed by the Working Group on Avian Nomenclature of the International Ornithologists' Union. We have registered the article with ZooBank and we have the received the following LSID registration numbers from Zoobank: *krabbei* A77E1A34-6D32-420B-9BE0-2C54E5769E0B, *frankeae* 8947DB55-8013-401B-9E39-DEB2E158917B, and *whitneyi* C504C4E5-38A0-4DEA-BD4E-C54C68C53984.

LITERATURE CITED

Abadi, S., D. Azouri, T. Pupko, and I. Mayrose (2019). Model selection may not be a mandatory step for phylogeny reconstruction. Nature Communications 10:934.

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

Avendaño, J. E., A. M. Cuervo, J. P. López-O, N. Gutiérrez-Pinto, A. Cortés-Diago, and C. D. Cadena (2015). A new species of tapaculo (Rhinocryptidae: *Scytalopus*) from the Serranía de Perijá of Colombia and Venezuela. The Auk: Ornithological Advances 132:450–466.

Baldwin, J. W., and J. R. Drucker (2016). Nest and nestling data for the unnamed 'Ampay' Tapaculo *Scytalopus* sp. from Apurímac, Peru. Cotinga 38:9–13.

Benham, P. M., E. J. Beckman, S. G. DuBay, L. M. Flores, A. B. Johnson, M. J. Lelevier, C. J. Schmitt, N. A. Wright, and C. C. Witt (2011).

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Satellite imagery reveals new critical habitat for endangered bird species in the high Andes of Peru. Endangered Species Research 13:145–157.

Bickford, D., D. J. Lohman, N. S. Sodhi, P. K. Ng, R. Meier, K. Winker, K. K. Ingram, and I. Das (2007). Cryptic species as a window on diversity and conservation. Trends in Ecology & Evolution 22:148–155.

Block, N. L., S. M. Goodman, S. J. Hackett, J. M. Bates, and M. J. Raherilalao (2015). Potential merger of ancient lineages in a passerine bird discovered based on evidence from host-specific ectoparasites. Ecology and Evolution 5:3743–3755.

Bolger, A. M., M. Lohse, and B. Usadel (2014). Trimmomatic: A flexible trimmer for Illumina sequence data. Bioinformatics 30:2114–2120.

Bouckaert, R., J. Heled, D. Kühnert, T. Vaughan, C.-H. Wu, D. Xie, M. A. Suchard, A. Rambaut, and A. J. Drummond (2014). BEAST 2: A software platform for Bayesian evolutionary analysis. PLoS Computational Biology 10:e1003537.

Brewer, D. (2018). Birds New to Science: Fifty Years of Avian Discoveries. Bloomsbury Publishing, London, UK.

Cadena, C. D., and L. N. Céspedes (2020). Origin of elevational replacements in a clade of nearly flightless birds – most diversity in tropical mountains accumulates via secondary contact following allopatric speciation. In Neotropical Diversification: Patterns and Processes (V. Rull and A. C. Carnaval, Editors). Springer, Berlin, Germany.

Cadena, C. D., A. M. Cuervo, L. N. Céspedes, G. A. Bravo, N. Krabbe, T. S. Schulenberg, G. E. Derryberry, L. F. Silveira, E. P. Derryberry, R. T. Brumfield, and J. Fjeldså (2020). Systematics, biogeography and diversification of Scytalopus tapaculos (Rhinocryptidae), an enigmatic radiation of Neotropical montane birds. The Auk: Ornithological Advances 137:1–30.

Chapman, F. M. (1915). The more northern species of the genus *Scytalopus* Gould. The Auk 32:406–423.

Chapman, F. M. (1926). The Distribution of Bird-life in Ecuador. Bulletin of the American Museum of Natural History 55.

Cory, C. B., and C. E. Hellmayr (1924). Catalogue of Birds of the Americas and the Adjacent Islands. Field Museum of Natural History Publications 223, Zoological Series Vol. XIII part III.

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.

De Queiroz, K. (2007). Species concepts and species delimitation. Systematic Biology 56:879–886.

Fjeldså, J. (1991). The activity of birds during snow-storms in high-level woodlands in Peru. Bulletin of the British Ornithologists' Club 111:4–11.

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

Gill, F. and D. Donsker (Editors) (2019). IOC World Bird List (v9.2). https://doi.org/10.14344/IOC.ML.9.2

Graves, G. R. (1985). Elevational correlates of speciation and intraspecific geographic variation in plumage in Andean forest birds. The Auk 102:556–579.

Graves, G. R. (1988). Linearity of geographic range and its possible effect on the population structure of Andean birds. The Auk 105:47–52.

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

Guindon, S., J. F. Dufayard, V. Lefort, M. Anisimova, W. Hordijk, and O. Gascuel (2010). New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. Systematic Biology 59:307–321.

Ho, S. Y., and S. Duchêne (2014). Molecular-clock methods for estimating evolutionary rates and timescales. Molecular Ecology 23:5947–5965.

Hosner, P. A., M. B. Robbins, T. Valqui, and A. T. Peterson (2013). A new species of *Scytalopus tapaculo* (Aves: Passeriformes: Rhinocryptidae) from the Andes of central Peru. The Wilson Journal of Ornithology 125:233–242.

Hosner, P. A., M. J. Andersen, M. B. Robbins, A. Urbay-Tello, L. Cueto-Aparicio, K. Verde-Guerra, L. A. Sánchez-González, A. G. Navarro-Sigüenza, R. L. Boyd, J. Núñez, et al. (2015). Avifaunal surveys of the upper Apurímac river valley, Ayacucho and Cuzco departments, Peru: New distributional records and biogeographic, taxonomic, and conservation implications. The Wilson Journal of Ornithology 127:563–581.

IUCN (2019). The IUCN Red List of Threatened Species. Version 2019-2. http://www.iucnredlist.org. Downloaded on July 18, 2019.

Jankowski, J. E., S. K. Robinson, and D. J. Levey (2010). Squeezed at the top: Interspecific aggression may constrain elevational ranges in tropical birds. Ecology 91:1877–1884.

Kearns, A. M., M. Restani, I. Szabo, A. Schrøder-Nielsen, J. A. Kim, H. M. Richardson, J. M. Marzluff, R. C. Fleischer, A. Johnsen, and K. E. Omland (2018). Genomic evidence of speciation reversal in ravens. Nature Communications 9:906.

Kearse, M., R. Moir, A. Wilson, S. Stones-Havas, M. Cheung, S. Sturrock, S. Buxton, A. Cooper, S. Markowitz, C. Duran, and T. Thierer (2012). Geneious basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28:1647–1649.

Kessler, M., and S. K. Herzog (1998). Conservation status in Bolivia of timberline habitats, elfin forest and their birds. Cotinga 10:50–54.

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, Jr., Editor). Ornithological Monographs 48:47–88.

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

Lanfear, R., B. Calcott, S. Y. Ho, and S. Guindon (2012). PartitionFinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. Molecular Biology and Evolution 29:1695–1701.

Lanfear, R., P. B. Frandsen, A. M. Wright, T. Senfeld, and B. Calcott (2016). PartitionFinder 2: New methods for

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selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. Molecular Biology and Evolution 34:772–773.
Lægaard, S. (1992). Influence of fire on the grass páramo vegetation of Ecuador. In Páramo: An Andean Ecosystem under Human Influence (H. Balslev and J. L. Luteyn, Editors). Botanical Institute, University of Aarhus, Denmark. pp. 151–170.
Maurício, G. N., H. Mata, M. R. Bornschein, C. D. Cadena, H. Alvarenga, and S. L. Bonatto (2008). Hidden generic 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.
Mayr, E. (1942). Systematics and the Origin of Species from the Viewpoint of a Zoologist. Columbia University Press, New York, NY, USA.
Moritz, C., J. L. Patton, C. J. Schneider, and T. B. Smith (2000). Diversification of rainforest faunas: An integrated molecular approach. Annual Review of Ecology and Systematics 31:533–563.
Munsell Soil Color Charts (1994, 2000). Macbeth Division of Kollmorgen Instruments Corporation, New York, NY, USA.
Nores, M. (1986). Diez nuevas subespecies de aves provenientes de islas ecológicas argentinas. El Hornero 12:262–273.
Patton, J. L., and M. F. Smith (1992). mtDNA phylogeny of Andean mice: A test of diversification across ecological gradients. Evolution 46:174–183.
Peters, J. L. (1951). Check-list of Birds of the World. Vol. VII. Museum of Comparative Zoology, Cambridge, MA, USA.
R Core Team (2013). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org
Rahbek, C. (1997). The relationship among area, elevation, and regional species richness in Neotropical birds. The American Naturalist 149:875–902.
Rambaut, A., A. J. Drummond, D. Xie, G. Baele, and M. A. Suchard (2018). Posterior summarization in Bayesian phylogenetics using Tracer 1.7. Systematic Biology 67:901–904.
Remsen, J. V. (1984). High incidence of "leapfrog" pattern of geographic variation in Andean birds: Implications for the speciation process. Science 224:171–173.
Remsen, J. V., and W. S. Graves (1995). Distribution patterns of Buarremon Brush-finches (Emberizinae) and interspecific competition in Andean birds. The Auk 122:225–236.
Remsen, J. V., J. I. Areta, Jr., C. D. Cadena, S. Claramunt, A. Jaramillo, J. F. Pacheco, M. B. Robbins, F. G. Stiles, D. F. Stotz, and K. J. Zimmer (2019). A classification of the bird species of South America. http://www.museum.lsu.edu/~Remsen/SACCBaseline.htm
Salter, J. F., C. H. Oliveros, P. A. Hosner, J. D. Manthey, M. B. Robbins, R. G. Moyle, R. T. Brumfield, and B. C. Faircloth (2019). Extensive paraphyly in the typical owl family (Strigidae). The Auk: Ornithological Advances 137:1–15.
Schulenberg, T. S., D. F. Stotz, D. F. Lane, J. P. O'Neill, and T. A. Parker, III (2010). Birds of Peru. Princeton University Press, Princeton, NJ, USA.
Stamatakis, A. (2014). RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30:1312–1313.
Terborgh, J. (1977). Bird species diversity on an Andean elevational gradient. Ecology 58:1007–1019.
Tschudi, J. J. (1844). Avium conspectus quae in Republica Peruana reperiuntur et pleraeque observatae vel collectae sunt in itinere a Dr. I. I. de Tschudi. Archiv für Naturgeschichte 10:262–317.
Whitney, B. M. (1994). A new *Scytalopus* tapaculo (Rhinocryptidae) from Bolivia, with notes on other Bolivian members of the genus and the *magellanicus* complex. The Wilson Bulletin 106:585–614.
Whitney, B. M., M. Ferreira de Vasconcelos, L. F. Silveira, and J. F. Pacheco (2010). *Scytalopus petrophilus* (Rock Tapaculo): A new species from Minas Gerais, Brazil. Revista Brasileira de Ornitologia 18:73–88.
Zimmer, J. T. (1939). Studies of Peruvian birds. No. XXXII: The genus *Scytalopus*. American Museum Novitates 1044:1–18.
Zimmer, J. T. (1941). Studies of Peruvian birds. No. XXXVIII: The genera *Oreotriccus, Tyrannulus, Acrochordopus, Ornithion, Leptopogon, Mionectes, Pipromorpha,* and *Pyrocephalus*. American Museum Novitates 1126:1–25.

APPENDIX A

List of Round Skin Specimens Examined, by Species and Department

Parentheticals following each museum catalog number contain ancillary information, we indicate the sex of the specimen (m = male, f = female, u = unsexed), age if obviously not adult (j = full juvenile plumage, imm = immature, not fully juvenile plumage nor fully adult) and details about its examination/measurement if not completed by TSS/NKK: museum acronyms are: American Museum of Natural History, New York, NY (AMNH); Academy of Natural Sciences of Drexel University, Philadelphia, PA (ANSP); Centro de Ornitología y Biodiversidad, Lima, Peru (CORBIDI); Field Museum of Natural History, Chicago, IL (FMNH); University of Kansas, Lawrence, KS (KU); Louisiana State University, Museum of Zoology, Baton Rouge, LA (LSUMZ); Museo de Historia Natural de la Universidad Mayor de San Marcos, Lima, Peru (MUSM); University of New Mexico Museum of Southwestern Biology, Albuquerque, NM (MSB); Natural History Museum of Denmark, University of Copenhagen, Denmark (NHMD); and Smithsonian National Museum of Natural History, Washington, D.C. (USNM).

acutirostris: (57) **Amazonas:** LSUMZ 88134 (m), 88139 (f), 88140 (uns, juv), 88145 (uns, juv); **La Libertad:** LSUMZ 92519 (f), 92523 (m), 92524 (m), 92522 (m); **Huánuco:** FMNH 65729 (m), 287809 (m), 287935 (m), LSUMZ 74113 (m), 74124 (m), 80599 (m), 80600 (f), 113583 (m), 119016 (m), 119017 (m, subad), 128579 (m), 128590 (m), 128591 (m), 128592 (m), 128593 (m), 128594 (f), 128595 (f), 128596 (m), 128597 (m), 128598 (m), 128599 (f), 128600 (m), 128601 (m), 128602 (m), 128603 (f), 128604 (f), 128605 (m), 128606 (f), 128607 (f, juv) MSB 31581 (m), NHMD 80032 (f; imm), 80033 (m), 80034 (m), 80035

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(m), 80036 (m); **Pasco:** LSUMZ 128586 (m), 128587 (m), 128588 (f); **Junín:** KU 113886 (m), 113885 (m), 113883 (m), 113884 (m), 113882 (u), 125653 (u), LSUMZ 127654 (m), 179574 (m), CORBIDI 2558 (m; MBR), 2570 (m; MBR), 2603 (m; MBR).

affinis: (9) **Ancash:** ANSP 115281 (f), 115282 (f), 115283 (u), 115284 (m), LSUMZ 80597 (m), 80598 (u), 82008 (f). **Cajamarca:** LSUMZ 84980 (m), 84981 (m).

krabbei: (7) **Amazonas:** LSUMZ 88141 (f), 88131 (f), 88137 (f), 88143 (f); **Huánuco:** LSUMZ 74122 (m). **San Martín:** LSUMZ 174041 (m; Holotype), 174042 (m).

simonsi: (18) **Cusco:** CORBIDI D.Suscinibar 303 (m); LSUMZ 78578 (f), 78581 (m), NHMD 80029 (m), MSB 27116 (f); **Puno:** ANSP 103299 (m), 103300 (m), KU 115469 (m), 115470 (m), 115471 (m), LSUMZ 98397 (f), 98398 (m), 98399 (f), 98403 (f), 98404 (m), 98405 (f), 98407 (f), NHMD 80027 (f), 80027 (u; imm); CORBIDI MCCF278 (m; PAH), EAC56 (m; PAH), and WW546 (m; PAH).

altirostris: (15) **Amazonas:** ANSP 115272 (f), 115273 (m), 115274 (m; j/imm), 115280 (f; j); **Huánuco:** FMNH 299219 (m), LSUMZ 119019 (m); **La Libertad:** ANSP 115267 (f), 115268 (m), 115269 (m), 115270 (m), 115271(f), LSUMZ 92512 (m), 92520 (f; imm), 92525 (m), 92513 (m).

frankeae; (42) **Huánuco:** FMNH 65730 (f; imm), 65731 (f), 65732 (f), 65733 (f), 65734 (m), 67392 (f), LSUMZ 128608 (m), 128609 (f), 128610 (m), 128611 (f), 128612 (m), 128613 (m), 128614(f), 128615 (m), 128616 (m), 128617 (m), 128618 (f), 128619 (m), 128620 (m), 128621 (m), 128622 (m), 128623 (m), 128624 (m), 128625 (m), 128626 (m), 128627 (m; imm), 128628 (m), 128629 (m), 129607 (m), 129610 (u), MUSM 7333 (m; imm); **Pasco:** AMNH 174083 (m). **Junín:** CORBIDI 2525 (f), 2530 (f), 2543 (m), 2544 (f), 2576 (f; photos only), KU 113888 (m), LSUMZ 179575 (m), MUSM DFL2140 (m), MSB 31818 (m), 31819 (u).

whitneyi: (9) **Apurímac:** LSUMZ 179689 (m), MSB 33916 (m), NHMD 80025 (m), 80110 (m). CORBIDI K. Faust 60 (m; PAH). **Ayacucho:** KU 122547 (m), 122548 (f), CORBIDI PAH1231 (m; PAH), PAH1233 (m; PAH).

urubambae: (4) **Cusco:** KU 122622 (m; MBR) 122623 (m), KU 122624 (f), USNM 273702 (m), NHMD 80109 (m), AMNH 170765 (f; holotype, DFL), CORBIDI LCA2012-56 (m), KVG210 (m), MCCF498 (m).

schulenbergi: (14) **Cusco:** LSUMZ 78580 (f), NHMD 80007 (m; imm); **Puno:** LSUMZ 98394 (m), 98395 (m), 98396 (m), 98400 (m), 98401 (f), 98402 (m), 98406 (m), KU 115464 (f), 115465 (m), 115466 (m), 115467 (f), 115468 (f).

APPENDIX B

Sound Recordings Analyzed

Xeno-Canto is abbreviated XC, Macaulay Library ML, "Isler Archive" IA (IA recordings are available upon request from the recordist B. M. Whitney [kite1173@gmail.com]), primary song s, secondary song ss, call c, male m, female f.

acutirostris: (100): **Amazonas:** XC480722s, 144s, 145s; **San Martín:** XC468108s, 468109c; **La Libertad:** ML17254s, 17224s; **Huánuco:** ML28767excited call,s, 28774c, 28777c, 36057s, 40123c,s, 40145c, 40149c, 40150c, 40154s, 40155s, 40157c, 168647c/s, 168659s, 195137s, 195140s, 195151s, 195163s, 104959211s, 104960981c, XCXC20169/ML230213 (also XC20171/ML230214)ms, XC20172/ML230215 (also XC20175/ML230216)ms, XC20173/ML230217ms, XC20174excited song, XC20170/ML230219excited call, XC20176/ML230218ms, XC20177/ML230220ms, XC388074mc,ms, 34393c, 40526c, 40527s, 40528s, 102436s, 102437s, 105226s, 142096s, 142323c,s, 142325c, 148511s, 229426c, 229427s, 229428c, 229430fs,s, 229431s, 229432s, 229433s, 229434s, 229435s, 296743s, 296744s, 296745s, 350674 (also 350675)s; **Pasco:** ML35904c, 35908s, 35925s, 35932c, 35962s, 35963c, 35981s, 35983s, 36015s, 40113s, XC27865s, 62935s, 65632s, 65636s; **Junín:** ML147220s, 147223c, 147235s, 147243c, 147258c, 147262s, 147300s,c,fs, 166390/171861s, 171844s, 171849c, 171850c, 171864fc,s, 207230c, 75025091s, 75029521s, 75029591s, 75047501s, 75049391c, XC152902c, 20657fc, 20662s, 61027c, 82628s, 88052s, 88053s, 88054c, 88055s, 88056c, 88057s, 468110c.

affinis: (27) **Ancash:** ML10468c, 11077c, 33960s, 208624s, 208647s, 208689s, 222085s, 238703s, 34179611c, 82179c, XC102367c, 12042s, 157529s, 16238s, 20178s, 20179fc, 20180c, 20181beggingcalls, 229436s, 256993s, 328105c, 350724s, 387836s, 43688s; **Lima:** ML161776c, 161778s; **Huánuco:** XC153754s.

krabbei: (9) **San Martín:** ML531454c, XC237624/ML531469(Holotype)c, XC237636/ML531470c, XC237637s; **Amazonas:** XC470184s; **Huánuco:** ML104960821c, XC20182s, 46780c, 46782c.

simonsi: (30) **Cusco:** IA10834s, ML17600c, 40173c, 100969s, 143675 c, 143691s, 171137s, 171139s, 516940s, 59776901s, XC229604s, 229605*brzk*-call,s, 229606excited call, 36120s, 47788 (also 47789)c,s,excited call, 90495s, 91745s, 92337s; **Puno:** ML148140s, XC47790s,fc; *n* **La Paz:** IA5419excited call, IA5420s, IA5421s, ML96838excited call, 96841s,fc, 63423941c, XC2139 mc,fsong, 74176s, 74177c.

altirostris: (10) **Amazonas:** XC147s, 40729s, 102393s, 102394s, XC115772–74/ML31953431s; **San Martín:** XC468093s, 468094s; **Huánuco:** XC229437(1st indiv.)s, 229437(2nd individ.)s, XC229438s.

frankeae (37): **Huánuco:** ML36058s, 40130s, 195139s, 195147s,f-brzk-call, 195148(Holotype)s, 195149s, 195156s. **Junín:** ML147226(Holotype)s, 161726s, 161727s, 166386s, 166387c, 166388single-churr, 166389single-churr, 171802s, 171855s, 171881s, 75052641s, 75052691s, 75054531(1st indiv,)s, 75054531(2nd indiv,)s, 75060681s, 75061671s, XC102389s, 152958s, 20431s, 20666s, 229607s, 229609s, 229610s, 29837single-churr, 350374s, 41106s, 41108single-churr, 82631s, 82668s, 468111s.

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whitneyi (33): **Apurímac:** ML128964c, 128965s,fc, 128966c, 129544ss,s, 129545ss,s, 27249131s (also 27249641 and 27250361), 27250391s, 27257931s, 75262521ss,s, 75262571s, XC20898s, 33861ss, 36107ss, 36108s, 74412–13s, 90570s, 102365s, 102366s, 333300ss, 404224s, XC436055/ML230279(1st indiv.)s (also XC436058), XC436055/ML230279(2nd indiv. Holotype)s (also XC436056–57), XC436059c, 468163s, 468166ss, 468184ss, 506637s; **Ayacucho:** ML140715s, 186900s, 186901s, 29966871s, 186928s,ss, 186931s.

urubambae: (21) **Cusco:** ML173949c, 173950ms, 173951s, 173987c, 173991c, 173992c, 186956ms, 186970ms, 197229s, XC73813–14s, 41578s, 41579s, 468095c,s, 468096s, 468097c,s, 468098s,excited call, 468099c, 468100s, 468102c, 468103c, 468104c.

schulenbergi: (31) **Cusco:** ML30404s, 32009s, 35431ss, 35432c, 40169s,c, 53501s, 100966c, 143688s, XC6893c, 20185s, 31979s, 229602s, 229603s, 507914s, 507915c, 507916c, 507918s/ss; **Puno:** ML148116c, 148117s, 148118s, 148123s, 148138s,*brzk*-call, 43782241s,c, 43782241s,c, 43865861s, XC20184c; *n* **La Paz:** ML96839s, 96840s, XC3503c, 3647c, 3648s.

APPENDIX C

Fieldwork and Study Sites

Amazonas: In August–September 1978, TSS (Louisiana State University Museum of Natural Science; LSUMZ) collected unassignable *S.* [*magellanicus*] at Cordillera Colán; in October 2012, FA recorded vocalizations of this form in the same cordillera. In October 2012 and October 2016, AJS recorded *S.* [*magellanicus*] vocalizations at Abra Barro Negro.

San Martín: In June–August 2002, DFL and TV (LSUMZ/Museo de la Universidad Mayor de San Marcos; MUSM) collected specimens and recorded vocalizations of *S.* [*magellanicus*] at Cerro Patricia.

Huánuco: In November 1983, NKK and JF (Natural History Museum of Denmark; NHMD) recorded *Scytalopus* vocalizations at Bosque Unchog. This site was visited by several LSUMZ expeditions in the 1970s–1980s; in July 1984, GHR collected *S.* [*magellanicus*] here. In July–August 1985, KVR, GHR, TJD, and TSS (LSUMZ) collected specimens and recorded vocalizations of an unknown *S.* [*magellanicus*] species near Millpo on the Huánuco/Pasco border. Until recently, this locality was believed to be in the Pasco department. In December 2009 and November 2013, AJS recorded *S.* [*magellanicus*] vocalizations at Bosque Unchog. In May 2010, June 2015, and June 2018, DFL recorded additional *S.* [*magellanicus*] vocalizations at Bosque Unchog.

Junín: In September 2004, June 2008, and March 23, 2010 (with TSS), DFL (LSUMZ/University of New Mexico Museum of Southwestern Biology; MSB/Centro de Ornitología y Biodiversidad; CORBIDI), collected *S.* [*magellanicus*] and recorded vocalizations at Chilifruta. In September–October 2008, PAH and MBR (University of Kansas Biodiversity Institute; KU/CORBIDI) collected *S.* [*magellanicus*] specimens and recorded vocalizations at Toldopampa.

Ayacucho: In December 2008, MJA and PAH, (KU/CORBIDI) recorded *S.* [*magellanicus*] vocalizations above Chungui and Anco. In September 2012, PAH recorded vocalizations and specimens above Chungui and near Chupón.

Apurímac: In March 1987, NKK and JF collected *S.* [*magellanicus*] and recorded vocalizations north of Abancay at Cerro Turronmocco. In November–December 1989, JF recorded vocalizations at Bosque Ampay and also found the species in the highlands southeast of Abancay at Runtacocha, Quebrada Balcón, and Quebrada Chua. In November 2004, PAH recorded *S.* [*magellanicus*] at Bosque Ampay. In June 2007, DFL (LSUMZ/CORBIDI) collected specimens and recorded vocalizations at Cerro Turronmocco.

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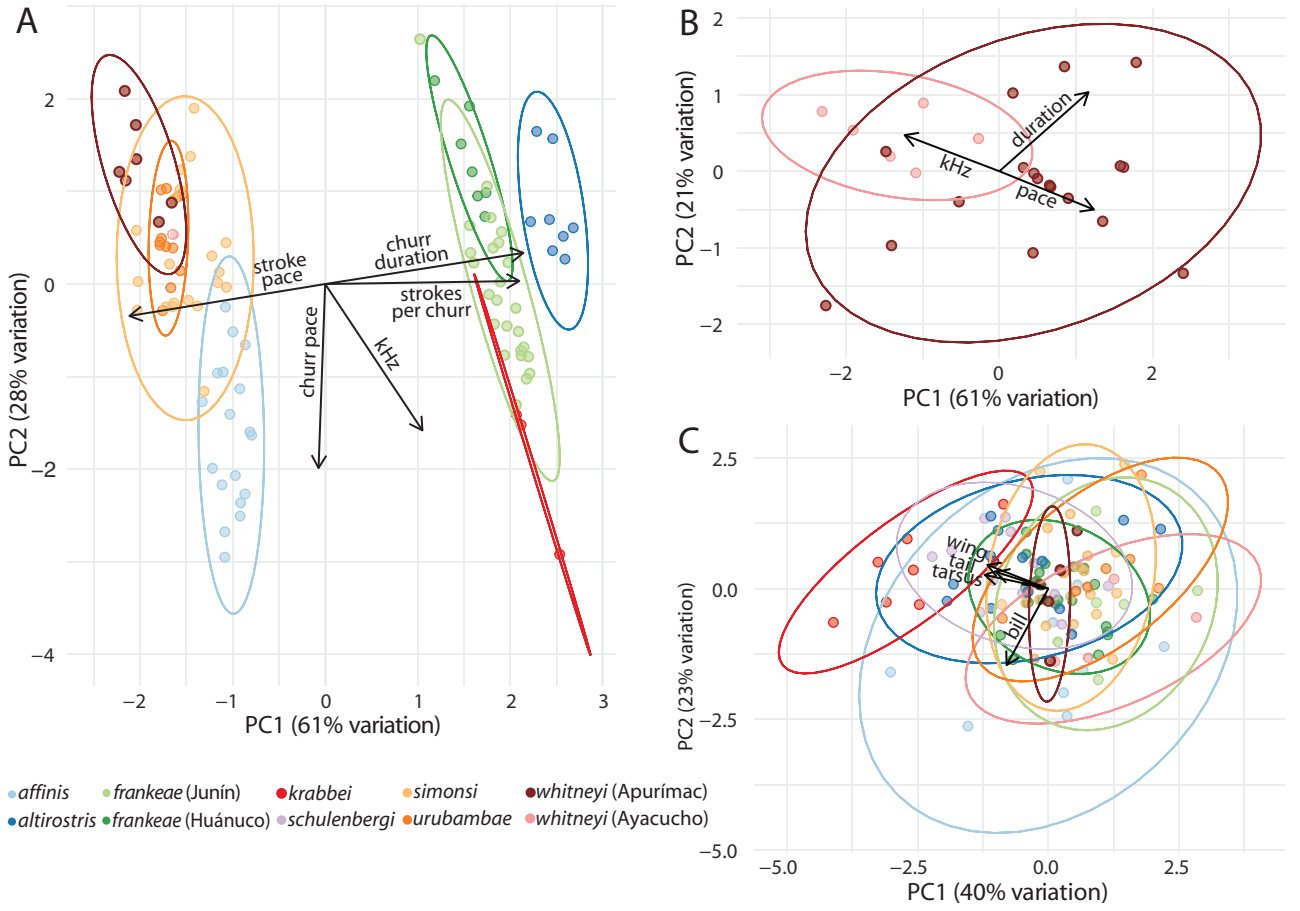

APPENDIX FIGURE 7. Principal component biplots of selected central Peruvian *Scytalopus* [*magellanicus*] vocal and morphological characteristics. Ellipses around point clouds define 95% confidence. (A) Principal component biplot of *S.* [*magellanicus*] churred songs, including the variables frequency at peak volume (kHz), pace (number of churrs per second), duration of churr, duration of each stroke in a churr. Species generally occupy unique areas of PC1/PC2 space, and those which overlap substantially (e.g., *S. simonsi*, *S. urubambae*) differ in additional qualitative characteristics. *S. schulenbergi* is not included because its song is structurally distinctive and difficult to compare meaningfully with other taxa represented. (B) Principal component biplot of primary (single-noted) songs of *S. whitneyi* from Apurímac and from Ayacucho. There is considerable overlap, but Ayacucho songs were on average higher pitched and slower paced. Variables include frequency at peak volume (kHz), pace (number of notes per second), and duration of single notes. (C) Principal component biplot of central Peruvian *Scytalopus* [*magellanicus*] morphological characteristics. Wing, tail, and tarsus measurements are highly correlated. All taxa overlap almost entirely, with the exception of *S. krabbei*, which is slightly larger than other taxa.

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