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Authors: Renjifo, Luis Miguel, Repizo, Augusto, Ruiz-Ovalle, Juan Miguel, Ocampo, Sergio, and Avendaño, Jorge Enrique

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New bird distributional data from Cerro Tacarcuna, with implications for conservation in the Darién highlands of Colombia

by Luis Miguel Renjifo, Augusto Repizo, Juan Miguel Ruiz-Ovalle, Sergio Ocampo & Jorge Enrique Avendaño

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SUMMARY.—We conducted an ornithological survey of the Colombian slope of Cerro Tacarcuna, the highland region adjacent to the ‘Darién Gap’ on the Colombia / Panama border, and one of the most poorly known and threatened regions in the world. We present novel data on distribution, habitat, breeding biology and vocalisations for 27 species, including the first confirmed records in Colombia of Ochraceous Wren *Troglodytes ochraceus* and Beautiful Treerunner *Margarornis bellulus*, and the first records in the Darién highlands of Black-headed Antthrush *Formicarius nigricapillus*, Scaly-throated Foliage-gleaner *Anabacerthia variegaticeps*, Yellow-throated Chlorospingus *Chlorospingus flavigularis hypophaeus* and, based on previously overlooked specimens, report the first confirmed records for Colombia of Sooty-faced Finch *Arremon crassirostris*. In addition, we collected the first Colombian specimens of Violet-capped Hummingbird *Goldmania violiceps*, Bare-shanked Screech Owl *Megascops clarkii*, Tacarcuna Tapaculo *Scytalopus panamensis* and Varied Solitaire *Myadestes coloratus*. For several subspecies endemic to the region, we collected the first or second specimens for Colombia. Finally, we discuss the elevational ranges of Darién endemic species and subspecies, which are mostly concentrated above 600 m. The Darién highlands remain poorly studied and threats to their conservation are increasing. Therefore, effective measures are needed, particularly in Colombia, where the sole protected area in the region currently covers forests only below 600 m.

The Darién comprises a system of humid lowlands dissected by mountain ranges and isolated massifs of moderate elevation, at the junction between Central and South America on the Colombia–Panaman border (Fig 1)—the so-called ‘Darién Gap’. The region has played a significant role in the biogeography and diversification of the Neotropics, serving as a route for or barrier to the exchange of Central and South American faunas during the Tertiary and Pleistocene (Simpson 1950, Mayr 1964, Haffer 1970, Smith & Klicka 2010). This interchange and isolation are evidenced by several lowland birds and contact zones between taxa with origins in Central America, the Chocó, Nechí, Magdalena Valley and Amazonia (Haffer 1967a,b). Likewise, several highland bird species from the Talamanca Mountains and West Andes of Colombia meet in the Darién. Some are recognised as subspecies or represent separate evolutionary lineages (Wetmore 1965, 1968, 1973, Wetmore *et al.* 1984, Miller *et al.* 2007, Cadena & Cuervo 2010, Gutiérrez-Pinto *et al.* 2012). Some authors have proposed the existence of isolated forest refuges on the slopes of several massifs in the region (e.g. Cerro Pirre, Cerro Tacarcuna south to Los Saltos–El Limón and northern Baudó Mountains) during recent geological history (Haffer 1967, Hernández-Camacho *et al.* 1992) as drivers of the high degree of avian endemism and population differentiation.

Current knowledge of Darién avifauna is incomplete (BirdLife International 2014) and mainly based on historical collections and observations, with better documentation

of lowland birds due to easier access (Rodríguez 1982, Hilty & Brown 1986, Ridgely & Gwynne 1989, Bayly *et al.* 2014, Hruska *et al.* 2016). In particular, the avifauna of the Gulf of Urabá, north-east of the Colombian Darién, has been studied in greater detail (Haffer 1959, 1967a,b, Bran-Castrillón *et al.* 2014). In contrast, the Darién highland avifauna has been less studied, although better documented on the Panamanian side, with expeditions to massifs such as Cerro Pirre, Alturas de Nique, Cerro Tacarcuna and its spur Cerro Malí (Wetmore 1965, 1968, 1973, Wetmore *et al.* 1984, Robbins *et al.* 1985, Ridgely & Gwynne 1989, Hruska *et al.* 2016), Altos de Quía (Wetmore & Galindo 1972), Serranía de Jungurudó (Angehr *et al.* 2004), Serranía de Majé (Angehr & Christian 2000) and the foothills of Cerro Piña (Miller *et al.* 2011), the last two of which are both isolated massifs north of the Serranía de Jungurudó. In Colombia, Cerro Tacarcuna has been the only Darién massif visited: H. E. Anthony and D. S. Ball in 1915 to the eastern slope of Alto Tacarcuna (Chapman 1917, Haffer 1959, Participantes de la Alianza Biomap 2006), L. Gualdrón *et al.* to Alto Barrigonal (c.1,400 m) in 1980 (specimens at Instituto Alexander von Humboldt, Villa de Leyva) and Pearman (1993) who ascended to 1,250 m in the headwaters of the río Tigre. Recent expeditions to the Serranía del Darién were conducted by J. Zuluaga-Bonilla in January 2007 to Cerro La Nevera (08°30'N, 77°26'W; c.475–775 m), municipality Acandí, dpto. Chocó; and by JMR-O & T. Walschburger in November 2008 to the headwaters of the río Tanelita at Cerro Tacarcuna (08°13'N, 77°16'W; c.1,250–1,400 m), Comunidad Eyákera, municipality Unguía, dpto. Chocó (Ruiz-Ovalle *et al.* 2014). Olaciregui *et al.* (2016) visited the Serranía de Abibe south-east of the Gulf of Urabá. Despite these new data, the paucity of field studies and the complex topography of the Colombian Darién makes this region one of the least biologically documented in the country (Rangel 2004, Arbeláez-Cortés 2013). It is expected that several bird species will be found on the Colombian side, representing range extensions from Panama and / or the Andes, some of them new species for the country and even South America.

Here, we present the results of an expedition to the Colombian slope of Cerro Tacarcuna in August 2010. We present a list of bird species recorded, several of which represent noteworthy range extensions, or additional records of poorly known species (e.g. endemics) from the Darién highlands of Colombia. Finally, we discuss the need for protection of the foothills and highlands of the Colombian Darién.

Methods

Three main mountain ranges run parallel from the eastern Isthmus of Panama to north-west Colombia (Fig. 1). On the Pacific slope, the Serranía de Jungurudó at 1,200 m ranges from its northern outlier, Cerro Sapó, south to the headwaters of the río Jaqué, and is connected to the Cordillera de Juradó and Altos de Aspavé. To the east, this serranía is separated from the Serranía de Pirre by c.30 km of lowlands in the valleys of the ríos Balsas and Juradó (Angehr *et al.* 2004). The Serranía de Pirre (1,550 m) extends further south to Alturas de Nique and Cerro Quía, and via a relatively high range connects to the Serranía de los Saltos (300–600 m) (Haffer 1970, Angehr *et al.* 2004). Nearly 50 km of lowlands separate the Pirre ridge from the Serranía del Darién on the Caribbean coast (Robbins *et al.* 1985). This range rises to 1,875 m at Cerro Tacarcuna and extends north to the Serranía de San Blas in Panama, terminating abruptly to the south-west at the Gulf of Urabá (Haffer 1970). Almost 100 km of humid lowlands of the Atrato Valley separate the Serranía del Darién from Serranía de Abibe (2,200 m), a northern spur of the West Andes of Colombia. The lower río Atrato drains into the Gulf of Urabá, forming an extensive delta covered by mangrove, riverine vegetation and flooded plains (Haffer 1970, Bran-Castrillón *et al.* 2014).

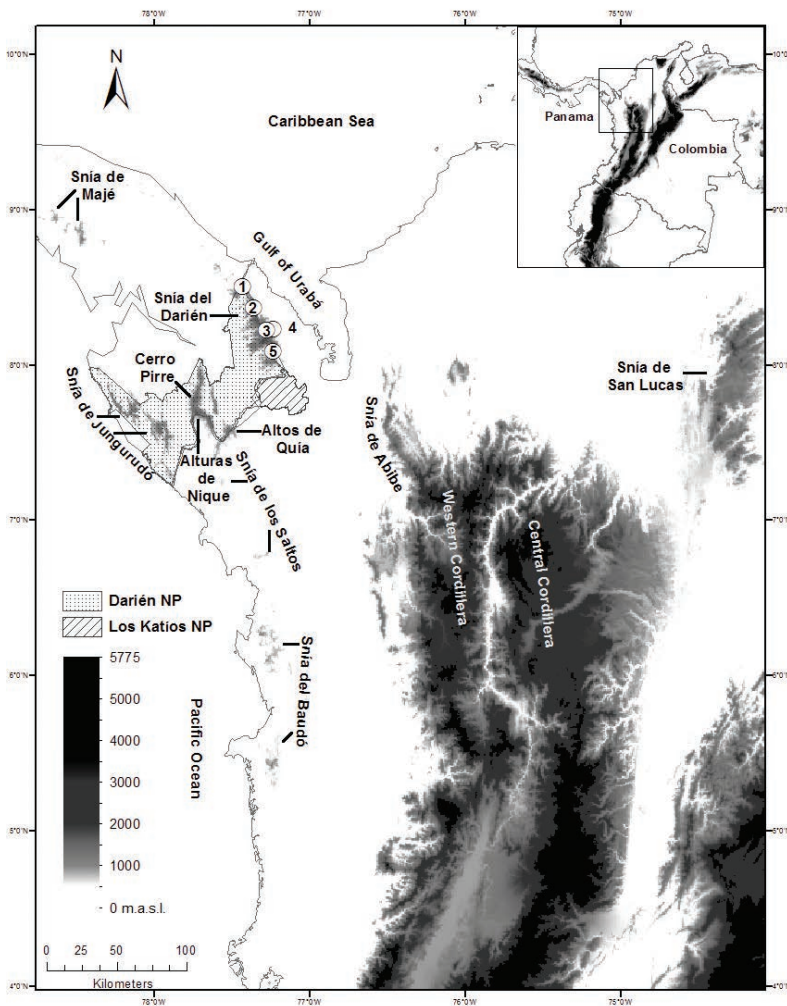


Figure 1. Map of north-western South America and eastern Panama showing the location of the Darién and the major geographical features mentioned in the text. Land above 600 m is indicated in grey to black. Circles represent historical and recent localities, including our study site in the Serranía del Darién: 1 = Cerro La Nevera (475–775 m), municipality Acandí, dpto. Chocó; 2 = Alto Barrigonal (1,400 m), municipality Acandí, dpto. Chocó; 3 = Cuchilla del Lago (1,150 m), Corregimiento de Balboa, municipality Unguía, dpto. Chocó; 4 = headwaters of the río Tanelita (1,250–1,400 m), Comunidad Eyákerá, municipality Unguía, dpto. Chocó; and 5 = headwaters of the río Tigre (1,250 m), municipality Unguía, dpto. Chocó.

We conducted field work along the ridge known as Cuchilla del Lago, Corregimiento de Balboa, municipality Unguía, dpto. Chocó, Colombia (08°13'49"N, 77°14'08"W; 1,150 m). The area lies in the headwaters of the río Bonito, on the east slope of the Cerro Tacarcuna (Fig. 1). We accessed Cuchilla del Lago by opening a trail in primary forest upslope from the left bank of the río Bonito (c.450 m), close to a property currently occupied by the Toro family. Based on our observations, the transition from wet to cloud forests on this part of Cerro Tacarcuna starts at c.900 m. Vegetation at our campsite comprised primary forest with a dense understorey and closed canopy 4–8 m tall, with many epiphytes and palms. Climate in this region is classified as partially dry according to annual precipitation (730–2,025 mm) and humidity (factor: -25–112), compared with wetter and more humid zones in southern Chocó (Poveda-M. *et al.* 2004).

Three observers made visual and aural records along two transects, between 05.45 h and 18.00 h on 4–7 August 2010. The first transect comprised c.300 m along the ridge at 1,150 m, which permitted us to sample different primary habitats (understorey, canopy facing the ridges and natural clearings). The second transect was at 980–1,150 m and followed the trail we opened to reach the campsite. Simultaneously, two of us undertook c.288 mist-net hours (12 × 2 m; 36 mm mesh) along the first transect, mainly between 06.00 h and 14.00

h. In addition, two observers made sound-recordings using Sony MiniDisc and Zoom-H4 digital recorders with Sennheiser ME-67 shotgun microphones. Recordings are deposited at www.xeno-canto.org (see Results). We collected some specimens that were mist-netted and others using a Gamo air rifle. Study skins are deposited in the ornithological collection of the Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá. Muscle tissue samples from each specimen were preserved in 95% Ethanol and deposited at Banco de Tejidos, Universidad de los Andes, Bogotá.

Results

We recorded 84 species in the cloud forest belt at 900–1,150 m. An additional 11 forest species were recorded at 450–900 m (Appendix 1). Of these, significant new distributional data or range extensions are presented for 27 species. Most (16) were expected to occur on the Colombian slope of Cerro Tacarcuna, given that they have been recorded on the Panamanian slope of Cerro Tacarcuna and adjacent Cerro Malí. However, seven species represent range extensions from other Darién massifs in Panama, the Serranía de San Blas, the Chocó lowlands, Serranía de Abibe and / or Western and Central Andes of Colombia. Another four records correspond to rare and poorly known species in Colombia, but previously known from Cerro Tacarcuna.

BARRED HAWK *Morphnarchus princeps*

Adult perched at 4–5 m near the campsite on 8 August 2010. Previously known from the Darién highlands on Cerro Pirre at 1,100–1,500 m (Wetmore 1965, Robbins *et al.* 1985) and Cerro Tacarcuna at 1,380 m (Sullivan *et al.* 2009), as well as locally on the Pacific slope of the West Andes from Quibdó south and in other Andean cordilleras (Hilty & Brown 1986).

RUSSET-CROWNED QUAIL-DOVE *Geotrygon goldmani*

Recorded by voice almost daily at 1,150 m near our campsite, but apparently in smaller numbers or was less vocal than Violaceous Quail-Dove *G. violacea*. Known from several localities in Panama, at Cerro Sapo (900 m), Cerro Pirre (900–1,600 m), Cerro Malí and Cerro Tacarcuna (1,450 m; Wetmore 1968), and recently the Serranía de Jungurudó (Angehr *et al.* 2004) and Cerro Piña (c.1,100 m; Miller *et al.* 2011). In Colombia, it is known only from the headwaters of the río Cutí on Cerro Tacarcuna and the río Juradó (c.90 m) in Chocó (Hilty & Brown 1986).

VIOLACEOUS QUAIL-DOVE *Geotrygon violacea*

One at 1,100 m vocalising from a 2 m-high perch. Known from the lower northern slopes of Cerro Pirre above Cana and El Real, and Cerro Sapo in Panama (Wetmore 1968, Ridgely & Gwynne 1989). In Colombia, known from a few records in the northern Central Andes and Serranía de San Lucas (Hilty & Brown 1986, Salaman *et al.* 2002).

BARE-SHANKED SCREECH-OWL *Megascops clarkii*

A pair recorded daily at 1,150 m (XC184848). Both individuals were perched in the midstorey (4–6 m) inside forest and usually started to vocalise at dusk. An adult male sound-recorded and collected (ICN 38187, XC184846) near the base camp on 7 August 2010. Hilty & Brown (1986) mentioned a specimen for Colombia, however, ours seems to represent the first confirmed Colombian record (Participantes de la Alianza Biomap 2006). The individual showed moderate body, wing and tail moult, with relatively large testes (left 5.0 × 1.7 mm). Stomach contents included parts of beetles (Coleoptera). *M. clarkii* is rare in Panama, with records at 1,080–2,100 m (Ridgely & Gwynne 1989). Previously known from Cerro Malí

(1,450 m), the crest of the Cerro Tacarcuna ridge (1,460 m, in both Panama and Colombia) and Cerro Pirre (Wetmore 1968) where it is rare to uncommon at 1,000–1,500 m (Robbins *et al.* 1985).

VIOLET-CAPPED HUMMINGBIRD *Goldmania violiceps*

Two females mist-netted at 1,150 m, of which one was collected (ICN 38179; Fig. 2). The specimen had an enlarged ovary (5.4 × 2.4 mm) with follicles averaging 0.3 mm, and no moult. Another four specimens (ICN 37362–65) were collected by JMR-O in November 2008 at the río Tanelita (c.1,400 m), c.4 km west of our study site (Fig. 1). Known from the foothills (600–1,200 m) of central and eastern Panama to Cerro Malí and Cerro Tacarcuna (Wetmore 1968, Ridgely & Gwynne 1989). In Colombia, previously known only from the headwaters of the río Cutí at Cerro Tacarcuna near the Panama border (Hilty & Brown 1986).

RED-HEADED BARBET *Eubucco bourcierii*

A male following a mixed-species canopy flock near our campsite. Although known in Panama from the foothills and highlands of Cerro Pirre, Cerro Quía, Cerro Malí and Cerro Tacarcuna (c.550–1,450 m; Wetmore 1968, Robbins *et al.* 1985, Ridgely & Gwynne 1989), this is the first confirmed record in the Colombian Darién (Hilty & Brown 1986). Recorded in the northern Central Andes, Serranía de San Lucas and the adjacent West Andes (Salaman *et al.* 2002, McMullan & Donegan 2014).

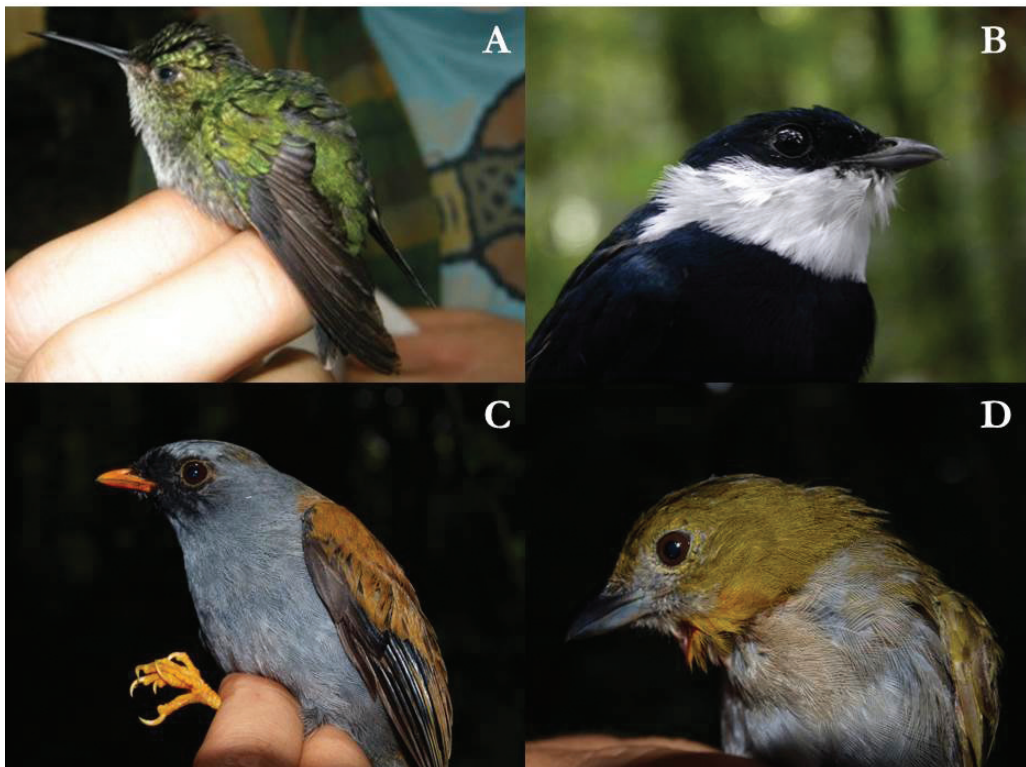


Figure 2. Restricted-range and noteworthy birds from Cerro Tacarcuna: (A) female Violet-capped Hummingbird *Goldmania violiceps*; (B) male White-bibbed Manakin *Corapipo leucorrhoa*; (C) Varied Solitaire *Myadestes coloratus*; (D) Yellow-throated Chlorospingus *Chlorospingus flavigularis* (J. M. Ruiz-Ovalle)



Figure 3. Ventral, dorsal and lateral views of adult male *Scytalopus tapaculos* in the Darién highlands and adjacent Western Andes of Colombia, from left to right: Nariño Tapaculo *S. viciniior* (ICN 31208), Alto de Pisones, 8 km north-west Jegüadas, municipality Mistrató, dpto. Risaralda, 6 June 1992; Tacarcuna Tapaculo *S. panamensis* (ICN 38181), Cuchilla del Lago, Corregimiento de Balboa, municipality Unguía, dpto. Chocó, 6 August 2010; and Chocó Tapaculo *S. chochoensis* (ICN 37480), Reserva Natural Río Nambí, Corregimiento de Altaquer, municipality Barbaocoas, dpto. Nariño, 11 October 2009 (J. E. Avendaño)

ZELEDON'S ANTBIRD *Myrmeciza zeledoni*

Observed in mixed-species flocks following army-ant swarms with Spot-crowned Antvireo *Dysithamnus puncticeps*, Chestnut-backed Antbird *Poliocrania exsul*, White-cheeked Antbird *Gymnopithys leucaspis*, Ocellated Antbird *Phaenostictus mcleannani* and Black-headed Antthrush *Formicarius nigricapillus*. On 6 August 2010, an adult male was foraging with a juvenile displaying a yellow gape, suggesting that it had fledged recently. Previously known in Panama on Cerro Pirre (c.500–1,400 m) and Cerro Tacarcuna (c.730–1,040 m; Robbins *et al.* 1985, Ridgely & Gwynne 1989, Donegan 2012a), with records in Colombia from adjacent ridges such as Serranía de Abibe (1,500 m), Serranía de Baudó (c.900 m), the Chocó lowlands and adjacent West Andes (Hilty & Brown 1986, Donegan 2012a, Olacrigerui *et al.* 2016).

TACARCUNA TAPACULO *Scytalopus panamensis*

Common in dense understory of primary forest at 1,040–1,150 m, where at least five vocal individuals were heard daily along a 300 m-transect. Individuals were often seen foraging alone, mainly at ground level up to c.0.5 m. Most were on slightly steep and humid slopes, close to fallen trunks and thickets. An adult male was attracted by its own song using playback, and collected, on 6 August 2010 (ICN 38181; Fig. 3). This is the first specimen for Colombia, although Pearman's (1993) sound recordings published in Krabbe & Schulenberg (1997) mean that it is already treated as a confirmed species for the country. It had small gonads (left testis 1.8 × 0.4 mm), but a fresh incubation patch and symmetric moult on its second primary. Our observations and previous studies on the Serranía del Darién suggest that *S. panamensis* is the only tapaculo on the Cerro Tacarcuna–Malí and adjacent slopes at 1,050–1,500 m (Wetmore 1972, Hilty & Brown 1986). We did not find Chocó Tapaculo *S. chochoensis*, which has been recorded on Cerro Pirre (1,350–1,475 m) and Serranía de Jungurudó (c.800–1,000 m) (Angehr *et al.* 2004), and along the Pacific foothills of the West Andes in Colombia and Ecuador, where it occurs at 250–1,250 m (Krabbe & Schulenberg 1997). The vocalisations of *S. panamensis* are hardly known (Krabbe & Schulenberg 1997, 2003). We recorded one call type (XC184857–58, 184860) and its primary song (XC184864, 184866, 184868). The call of *S. panamensis* is a rapid series of 5–6 up-downstrokes, lasting 0.6–0.8 seconds, and repeated every 1.5–4.0 seconds for up to 13.0 seconds, with a max. frequency of 4.0 ± 0.4 kHz (mean and standard deviation, respectively; Fig. 4A). Krabbe & Schulenberg (1997) suggested some similarity between the calls of *S. panamensis* and *S. chochoensis* (Fig. 4B) based on a tape-recording by Pearman (1993). However, the call of *S.*

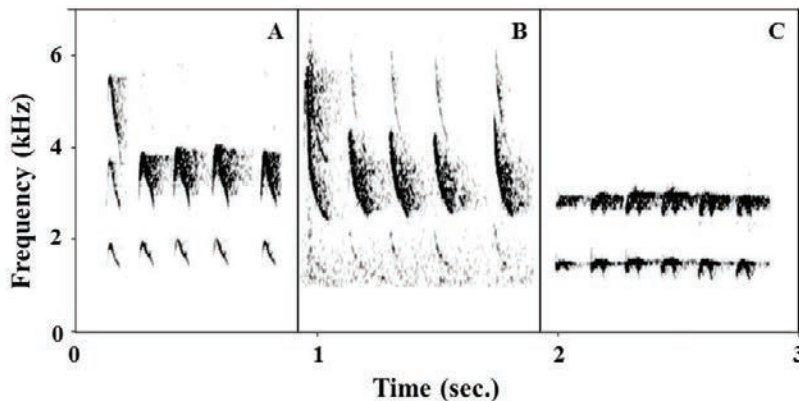


Figure 4. Calls of *Scytalopus tapaculos* from Darién and the West Andes of Colombia: (A) Tacarcuna Tapaculo *S. panamensis* natural vocalisation (XC184857, J. E. Avendaño), Cuchilla del Lago, Corregimiento de Balboa, municipality Unguía, dpto. Chocó; (B) Chocó Tapaculo *S. chocoensis* natural vocalisation (BSA 11716; Álvarez *et al.* 2007), Tambito Nature Reserve, municipality El Tambo, dpto. Cauca, Colombia; (C) Nariño Tapaculo *S. viciniior* natural vocalisation (BSA 30763; Álvarez *et al.* 2007), Las Nubes Nature Reserve, municipality Jericó, dpto. Antioquia. Note the distinctive frequency bandwidth and note shape in *S. panamensis*. Spectrograms were created using Syrinx v2.6h (Burt 2006) applying the same parameters except for adjusting brightness to improve note resolution.

chocoensis has a mean higher variation in frequency (the difference between max. and min. frequencies; 2.0 ± 0.4 kHz, $n = 6$ vs. 1.2 ± 0.2 kHz, $n = 3$) and comprises sharp notes. The call of Nariño Tapaculo *S. viciniior* (Fig. 4C) also differs from that of *S. panamensis* in its mean lower max. frequency (3.2 ± 0.2 kHz, $n = 7$) and note shape (e.g. length of stroke 'tails'). A natural song of *S. panamensis* was a 16.2-second series of 0.05–0.06-second up-downstroke notes delivered at 3.7 notes / second on average. During playback responses (Fig. 5A), the song was prolonged and faster (lasting 18.8–32.1 seconds and delivered at 4.5–4.7 notes / second, $n = 2$). Note shape is similar to that of some individuals of *S. chocoensis* (Fig. 5B–C), and differs from the downstroke notes of *S. viciniior* (Fig. 5D). It also is faster paced than *S. chocoensis*, but slower than *S. viciniior*. Thus, *S. panamensis* appears to be a vocal and morphologically distinct taxon (Fig. 3), although it overlaps in some vocal attributes with *S. viciniior* and *S. chocoensis*, suggesting that they are closely related. Vocalisations referenced herein are detailed in Appendix 2.

BLACK-HEADED ANTTHRUSH *Formicarius nigricapillus*

Solitary individuals, or with mixed-species flocks, observed following army-ant swarms above 1,000 m at our study site. Previously recorded in the Chocó lowlands at Nuquí north to Bahía Solano (D. Calderón-F. pers. comm.), the río Jurubidá on the Pacific coast (Haffer 1967a, Hilty & Brown 1986) and Serranía de Abibe (D. Calderón-F. pers. comm.). The closest locality in Panama is Nusagandi, western San Blas (Ridgely & Gwynne 1989). Black-faced Antthrush *F. analis* inhabits the Urabá region and the Atrato Valley, but the contact zone between the two species was not previously known. Haffer (1967a) suggested the Alto del Buey area (1,810 m), in the Serranía del Baudó, as a possible contact zone. However, one record of Black-faced Antthrush on the Panamanian slope of Cerro Tacarcuna at 1,180 m (Sullivan *et al.* 2009), plus an aural record below 800 m at our study site suggests possible contact in the foothills of Cerro Tacarcuna, where the species possibly replace each other elevationally. Specimen collection will be necessary to test Haffer's hypothesis that the two species may hybridise in a narrow zone within this region.

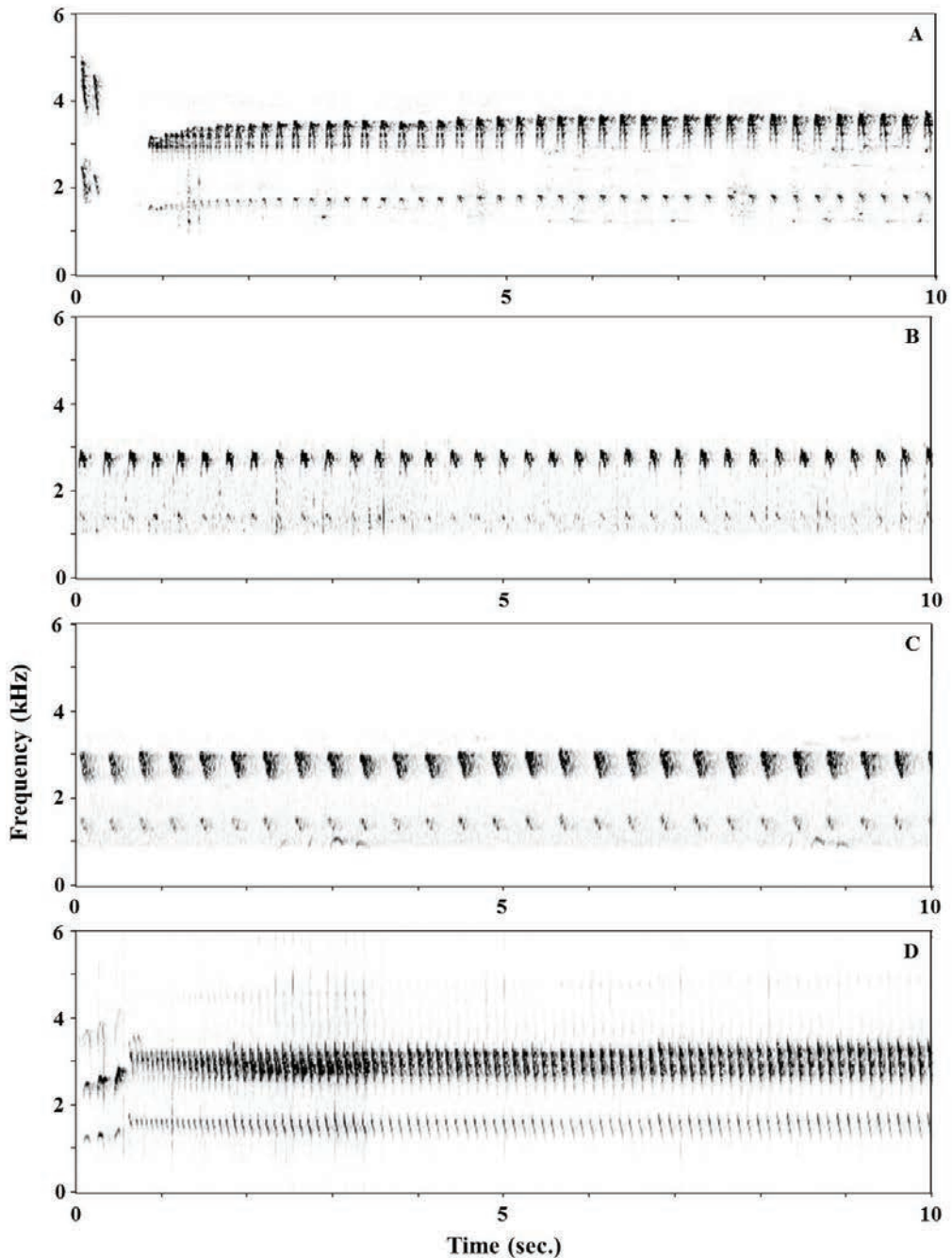


Figure 5. Primary songs of *Scytalopus* tapaculos from Darién and the Andes of Colombia and Ecuador: (A) Tacarcuna Tapaculo *S. panamensis* song after playback (XC184866, J. E. Avendaño), Cuchilla del Lago, Corregimiento de Balboa, municipality Unguía, dpto. Chocó, Colombia; (B) Chocó Tapaculo *S. chocoensis* natural song (LNS 40016, T. S. Schulenberg), El Placer, prov. Esmeraldas, Ecuador; (C) *S. chocoensis* natural song (XC60678, K. Allaire), Cerro Pirre, prov. Darién, Panama; (D) Nariño Tapaculo *S. viciniior* natural song (BSA 15041, Álvarez *et al.* 2007), Corregimiento de Bitaco, municipality La Cumbre, dpto. Valle del Cauca, Colombia.

SPOTTED WOODCREEPER *Xiphorhynchus erythropygius*

Singles or pairs observed daily in mixed-species flocks in the midstorey and subcanopy. Previously known in Panama from Cerro Pirre (1,580 m), Cerro Malí (1,450 m; Robbins *et al.* 1985, Wetmore 1972) and Serranía de Majé (c.1,150–1,250; Angehr & Christian 2000). Adjacent records in Colombia are from the Serranía del Baudó, ríos Atrato and Truandó (Participantes de la Alianza Biomap 2006), the Pacific slope of the West Andes (Hilty & Brown 1986), Serranía de Abibe (Olaciregui *et al.* 2016), the northern Central Andes (Cuervo *et al.* 2008b) and Serranía de San Lucas (Donegan 2012b).

BROWN-BILLED SCYTHEBILL *Campylorhamphus pusillus*

Observed and tape-recorded (XC184875) at 1,150 m. Previously known in Panama from Cerro Tacarcuna (1,250 m), Cerro Malí (1,460 m), Cerro Pirre (1,000–1,600 m), Cerro Quía (760 m; Wetmore 1972, Robbins *et al.* 1985) and Serranía de Majé (c.1,150–1,250 m; Angehr & Christian 2000). In Colombia, known from Serranía de Abibe (Olaciregui *et al.* 2016), the northern West Andes at Frontino (Hilty & Brown 1986) and the northern Central Andes (Cuervo *et al.* 2008b). Our record confirms the species' presence on the Colombian slope of the Tacarcuna massif.

SCALY-THROATED FOLIAGE-GLEANER *Anabacerthia variegaticeps*

Singles in canopy-level mixed-species flocks also containing Red-faced Spinetail *Cranioleuca erythrops* and several *Tangara* species. The nearest localities to our record are Cerro Flores in eastern Chiriquí, Panama (Ridgely & Gwynne 1989), and near Carmen de Atrato, Antioquia (D. Calderón-F. pers. comm.) and Serranía de Abibe at the northern extremity of the West Andes, Colombia (Olaciregui *et al.* 2016). Taxonomy of Middle and South American populations of this species is controversial, with some authors suggesting that *A. v. temporalis* of the West Andes should be recognised as a separate species from Middle American populations (Remsen *et al.* 2016). Specimens from the Darién will be crucial to resolve species limits in the group.

BEAUTIFUL TREERUNNER *Margarornis bellulus*

One on 5 August at 1,025 m, investigating vine tangles and epiphytes 4–5 m above ground. Its presence in Colombia was based on mainly habitat continuity and geographic proximity to known localities in adjacent Panama, e.g. Cerro Pirre (1,375–1,580 m), Cerro Malí (c.1,400–1,450 m) and Cerro Quía (900 m; Wetmore 1972, Ridgely & Gwynne 1989, Renjifo *et al.* 2002) and recently Serranía de Majé (1,150 m; Angehr *et al.* 2004). However, a 'Bogotá' specimen was recently reported (Verhelst-Montenegro 2015). Our record extends the species' range to Cerro Tacarcuna, and is the first confirmed locality for Colombia and South America (Remsen *et al.* 2016).

RUFOUS-BROWED TYRANNULET *Phylloscartes superciliaris*

Singles or pairs were seen within mixed-species flocks in the canopy. Previously known on the Panamanian side of Cerro Tacarcuna and Cerro Malí (1,060 m; Wetmore 1972, Ridgely & Gwynne 1989). In Colombia, this little-known bird has been recorded recently in the West Andes (Cuervo *et al.* 2003), Central Andes (Salaman *et al.* 2002, Cuervo *et al.* 2008a) and Serranía de San Lucas (Donegan 2012b), with historical records in the East Andes in dpto. Santander (Hilty & Brown 1986).

PIRATIC FLYCATCHER *Legatus leucophaeus*

Heard at 450 m beside the río Bonito. This record extends the species' range to the Gulf of Urabá, closing a gap between Cerro Pirre (600–1,000 m; Robbins *et al.* 1985), the Chocó lowlands and northern West Andes (Hilty & Brown 1986, Olaciregui *et al.* 2016). This is a widespread species of lowland habitats that has possibly colonised the region due to the expansion of modified environments.

WHITE-BIBBED MANAKIN *Corapipo leucorhoa*

Very common at 1,150 m where six males and four females were mist-netted (Fig. 2). Panamanian records are available from Cerro Pirre, Cerro Tacarcuna (575–1,250 m) and Cerro Quía (730 m) (Wetmore 1972, Ridgely & Gwynne 1989). The nearest localities in Colombia are the humid northern slopes of the West and Central Andes (Hilty & Brown 1986). The very similar White-ruffed Manakin *C. altera*, which also occurs on Cerro Tacarcuna and Cerro Malí, is present on adjacent mountains such as Cerro Pirre (1,050–1,375 m), Cerro Sapo, Jaqué (Wetmore 1972) and Serranía de Jungurudó (Angehr *et al.* 2004), as well as probably south along the Pacific coast to Serranía del Baudó (Hilty & Brown 1986). These taxa appear to be separate species based on their sympatry in this region, which is probably related to differences in the structure of their outer primaries, which may affect their respective displays (Ridgely & Gwynne 1989, Remsen *et al.* 2016). However, lek behaviour has been studied only in *C. altera* (Hilty & Brown 1986, Remsen *et al.* 2016).

OCHRACEOUS WREN *Troglodytes ochraceus*

Singles or pairs seen daily, foraging in the midstorey and subcanopy (3–4 m) at 1,150 m. They searched for insects within dense mosses and bromeliads, climbing vine tangles and inspecting dead, curled leaves trapped by vines, as part of mixed-species flocks formed mainly of tanagers and furnariids, although the wren also foraged and vocalised in the absence of other species. Two song types (XC184885, 184890) and one call (XC184888) were sound-recorded. These match recordings from Chiriquí province in Panama (Fig. 6) and clearly differ from vocalisations of Mountain Wren *T. solstitialis*, which occurs in the West Andes. This wren ranges from Costa Rica to Panama where it has been recorded on Serranía de Majé (c.1,150–1,490 m; Angehr & Christian 2000), Cerro Pirre (c.1,000–1,580 m; Robbins *et al.* 1985), and Cerro Malí (c.1,460 m; Wetmore *et al.* 1984). Our records confirm the species' presence in Colombia and South America for the first time (Donegan *et al.* 2016, Remsen *et al.* 2016).

VARIED SOLITAIRE *Myadestes coloratus*

One to three were heard daily and sound-recorded (XC184927). Singles took fruits from shrubs in the understorey at 1,100–1,150 m. An adult male was collected on 7 August 2010 (ICN 38185; Fig. 2); stomach contents included fruit and insect parts. The specimen had abundant moult in the body, wing and tail, and small testes (left 3.0 × 1.1 mm), which agrees with an immature collected on 29 August 1996 on Serranía de Majé (Angehr & Christian 2000). An additional specimen (ICN 37358) was collected by JMR-O in November 2008 at río Tanelita (c.1,400 m), on the east slope of Cerro Tacarcuna. This Darién highland endemic is known in Panama from Cerro Pirre (1,500–1,600 m), Alturas de Nique, Cerro Quía (900 m), Cerro Malí (1,400–1,600) (Ridgely & Gwynne 1989, Wetmore *et al.* 1984), and recently from Serranía de Majé (c.1,250–1,500 m) and Serranía de Jungurudó (c.1,000 m) (Angehr & Christian 2000, Angehr *et al.* 2004). Despite its broad distribution across isolated massifs in the Darién, and the apparent lack of phenotypic differentiation (Angehr & Christian 2000,

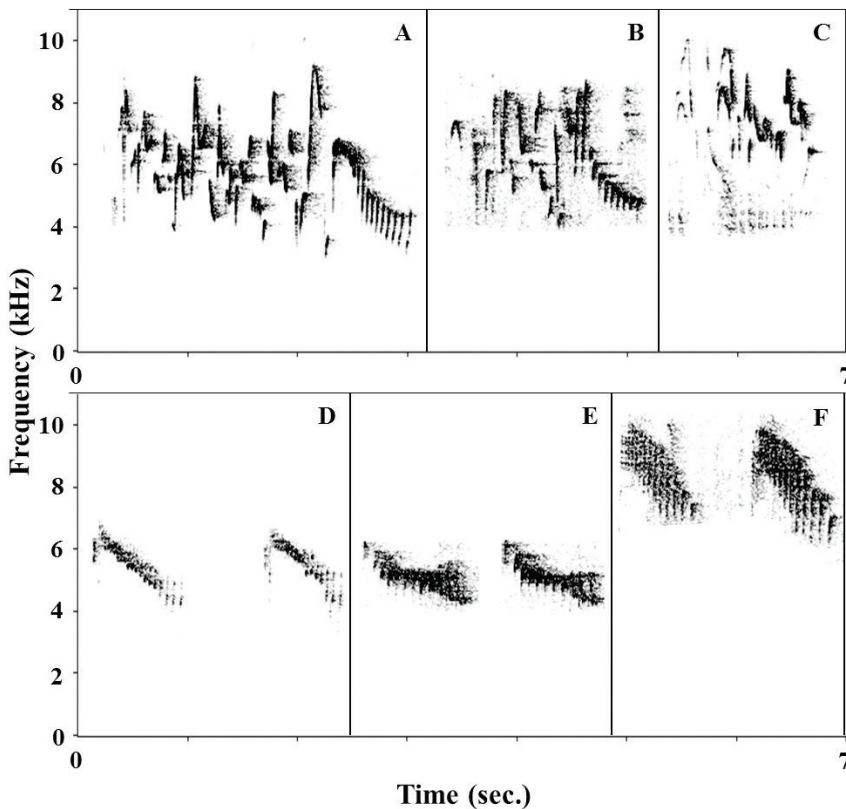


Figure 6. Songs and calls of *Troglodytes* wrens from Panama, Darién and the Andes of Colombia: (A) Ochraceous Wren *T. ochraceus* natural song (XC31764, A. Spencer), 2,300 m, Sendero Los Quetzales, prov. Chiriquí, Panama; (B) *T. ochraceus* natural song (XC184885, J. E. Avendaño), Cuchilla del Lago, Corregimiento de Balboa, municipality Unguía, dpto. Chocó, Colombia; (C) Mountain Wren *T. solstitialis* natural song (BSA 22470, Álvarez *et al.* 2007), Ibanasca, Corregimiento de Juntas, municipality Ibagué, dpto. Tolima, Colombia; (D) *T. ochraceus* natural call (XC94688, W. Adsett), 1,650 m, Cerro Colorado, Comarca Ngobe-Bugle, Panama; (E) *T. ochraceus* natural call (XC184888, J. E. Avendaño), Cuchilla del Lago, Corregimiento de Balboa, municipality Unguía, dpto. Chocó, Colombia; (F) *T. solstitialis* natural call (XC27530, N. Krabbe), Páramo de Frontino, dpto. Antioquia, Colombia.

Angehr *et al.* 2004), populations of *M. coloratus* on Cerro Pirre are genetically distinct from those of Serranía de Majé (Miller *et al.* 2007).

BLACK-AND-YELLOW TANAGER *Chrysothlypis chrysomelas*

A common and noisy member of mixed-species flocks at the campsite (1,150 m) where a family group of 3–4 individuals was seen daily, foraging in the canopy and feeding at least one fledgling. This group was often accompanied by other tanagers, *Chlorospingus* species, woodcreepers and tyrant flycatchers. Previously known in Panama on Cerro Tacarcuna (625–725 m), Cerro Sapo, Cerro Pirre, Cerro Quía (Ridgely & Gwynne 1989, Wetmore *et al.* 1984) and Serranía de Majé (Angehr & Christian 2000). Our records represent the third confirmed records for Colombia and South America. Previous records from Colombia are a female specimen (ICN 37353) collected by JMR-O in November 2008 at río Tanelita (c.1,400 m), on the east slope of Cerro Tacarcuna (Ruiz-Ovalle *et al.* 2014); and one observed by J. Zuluaga-Bonilla on Cerro La Nevera (c.475–775 m), c.37 km north-west of our study site in January 2007 (Fig. 1).

BLUE-AND-GOLD TANAGER *Bangsia arcaei*

Singles recorded daily at 1,150 m accompanying midstorey and subcanopy mixed-species flocks comprising insectivores and frugivores such as Slaty Antwren *Myrmotherula schisticolor*, Red-faced Spinetail, Olivaceous Woodcreeper *Sittasomus griseicapillus*, Ochraceous Wren, Speckled Tanager *Tangara guttata*, Bay-headed Tanager *T. gyrola*, Silver-throated Tanager *T. icterocephala*, Black-and-yellow Tanager, Yellow-throated Chlorospingus *Chlorospingus flavigularis* and Tawny-capped Euphonia *Euphonia annae*. This species ranges across the Caribbean slope from Costa Rica (400–1,200 m; Stiles & Skutch 1989) south to Panama (300–1,050 m), with the easternmost record from Cerro Brewster in western San Blas (Ridgely & Gwynne 1989, Wetmore *et al.* 1984). Our record represents the second for Colombia, following two specimens (ICN 37361, 37372) collected in November 2008 between 1,250 m and 1,400 m at río Tanelita, on the east slope of Cerro Tacarcuna (Ruiz-Ovalle *et al.* 2014).

BAY-HEADED TANAGER *Tangara gyrola*

Common in canopy-level mixed-species flocks. Previously known in Panama from Serranía de Majé, Cerro Sapo, Cerro Pirre, Cerro Malí, Cerro Tacarcuna (Wetmore *et al.* 1984) and Serranía de Jungurudó (Angehr *et al.* 2004). This record extends the species' range to the Colombian slope of the Cerro Tacarcuna. Adjacent records from Colombia are from Serranía de Abibe, the West Andes and northern Central Andes (Hilty & Brown 1986, Cuervo *et al.* 2008b, Olaciregui *et al.* 2016).

EMERALD TANAGER *Tangara florida*

Rare in canopy-level mixed-species flocks. Previously known in Panama from Cerro Pirre (Robbins *et al.* 1985), Cerro Tacarcuna (Wetmore *et al.* 1984) and Serranía de Jungurudó (Angehr *et al.* 2004); and Serranía de Abibe, south to El Carmen de Atrato in the West Andes of Colombia (Sullivan *et al.* 2009, Olaciregui *et al.* 2016). The Pacific slope subspecies is *T. f. auriceps*, whereas the nominate occurs on the Caribbean slope from Costa Rica to Panama. We were unable to collect specimens, consequently the subspecies in the Serranía del Darién is unknown, although it has been considered to represent an intermediate population (Haffer 1967a, Wetmore *et al.* 1984).

TACARCUNA CHLOROSPINGUS *Chlorospingus tacarcunae*

One of the commonest constituents of mixed-species flocks in the midstorey and subcanopy at 1,150 m (XC184939), moving in family groups of 4–5 individuals and frequently accompanied by Yellow-throated Chlorospingus *C. flavigularis*, which was more abundant. Both *Chlorospingus* appear to be core members of mixed-species flocks mainly comprised by Spotted Woodcreeper, Red-faced Spinetail, Green Manakin *Cryptopipo holochlora*, Scale-crested Pygmy Tyrant *Lophotriccus pileatus*, Rufous-browed Tyrannulet, Ochraceous Wren, Slate-throated Redstart *Myioborus miniatus*, Silver-throated Tanager, Black-and-yellow Tanager and Tawny-capped Euphonia. During our field work, a fledging was observed begging for food from an adult on 6 August 2010, which is consistent with previous observations of nest construction and immatures that suggest the species' breeding season probably begins in late February and extends to the middle of the year (Wetmore *et al.* 1984, Angehr & Christian 2000, Christian 2001). JMR-O collected one (ICN 37351) in November 2008 at 1,400 m at río Tanelita, on the east slope of Cerro Tacarcuna, representing the first specimen for Colombia. These are the only confirmed records in Colombia (*cf.* Donegan *et al.* 2011) of a species whose presence in the country had been suggested based on Panamanian records from Cerro Tacarcuna (1,230–1,440 m) and Cerro Malí (1,410 m) (Wetmore *et al.* 1984, Hilty & Brown 1986, Ridgely & Gwynne 1989).

YELLOW-THROATED CHLOROSPINGUS *Chlorospingus flavigularis*

Observed regularly in mixed-species flocks with *Tacarcuna chlorospingus* (see above). A fledgling was observed begging for food and an adult and juvenile mist-netted on 5 August 2010. The adult had brown irides and a buff breast (Fig. 2) matching descriptions of *C. f. hypophaeus*, which occurs in Bocas del Toro to Veraguas in Panama, in contrast to the grey eyes and breast of *C. f. marginatus* on the Pacific slope of the West Andes (Isler & Isler 1999). A specimen (ICN 37354), which also agrees with *C. f. hypophaeus*, was collected by JMR-O in November 2008 at 1,400 m on the río Tanelita, east slope of Cerro Tacarcuna. These records confirm this subspecies' presence on Cerro Tacarcuna and in Colombia for the first time. Its nearest locality is Cerro Brewster in western San Blas (Ridgely & Gwynne 1989). In Colombia the species occurs north to the upper río Sinú (Hilty & Brown 1986) and was recently recorded in Serranía de San Lucas (Donegan 2012b).

CHESNUT-CAPPED BRUSH FINCH *Arremon brunneinucha*

Fairly common in the understorey above 1,000 m. Previously recorded on most massifs on the Panamanian side, on Cerro Pirre, Cerro Quía (900 m), Cerro Tacarcuna, Cerro Malí (1,400 m) (Wetmore *et al.* 1984), Serranía de Majé and Serranía de Jungurudó (Angehr & Christian 2000, Angehr *et al.* 2004). Adjacent Colombian records are from the West Andes (Hilty & Brown 1986), the northern Central Andes (Cuervo *et al.* 2008b) and Serranía de San Lucas (Salaman *et al.* 2002).

SOOTY-FACED FINCH *Arremon crassirostris*

Status in Colombia and South America uncertain (Donegan *et al.* 2011, Remsen *et al.* 2016). Although we did not record the species, we report here two specimens collected in the foothills of Cerro Tacarcuna, at Alto Barrigonal, in June 1980. Both specimens, a male and female (IAvH-A 3164, 3174; Fig. 7) exhibit the conspicuous white malar stripe and yellow patch on the central underparts typical of the species. Based on these specimens, Rodríguez (1982) listed the species for Los Katíos National Park, as subsequently Hilty & Brown (1986) did for Colombia. On 1 December 2008 an unsexed specimen (ICN 37368) was collected by JMR-O & T. Walschburger at río Tanelita (1,408 m), on the east slope of Cerro Tacarcuna. These records remove any doubts concerning the species' presence in Colombia and South America (Remsen *et al.* 2016).

HEPATIC TANAGER *Piranga flava*

A male in a mixed-species canopy flock at the campsite. Panamanian records are from Darién province (Ridgely & Gwynne 1989), Serranía de Majé (Angehr & Christian 2000) and Cerro Pirre (Robbins *et al.* 1985). Nearest Colombian records are from the Pacific slope of the West Andes, in Serranía de Abibe south (Hilty & Brown 1986, Olaciregui *et al.* 2016).

Discussion

Despite field work during the last century, the Darién highland avifauna continues to be poorly known. Among the new distributional records here, ten relate to little-known and restricted-range species from the Darién highlands (Russet-crowned Quail-Dove, Bare-shanked Screech Owl, Violet-capped Hummingbird, Tacarcuna Tapaculo, Beautiful Treerunner, Ochraceous Wren, Varied Solitaire and Tacarcuna Chlorospingus) and foothills (Blue-and-gold and Black-and-yellow Tanagers), which represent 40% of the endemic species reported in the region (Fig. 8A). In addition, four species previously known from Panama were recorded for first time in the Darién highlands of Colombia. Two of these (Scaly-throated Foliage-gleaner and Ochraceous Wren) inhabit cloud forests of the West

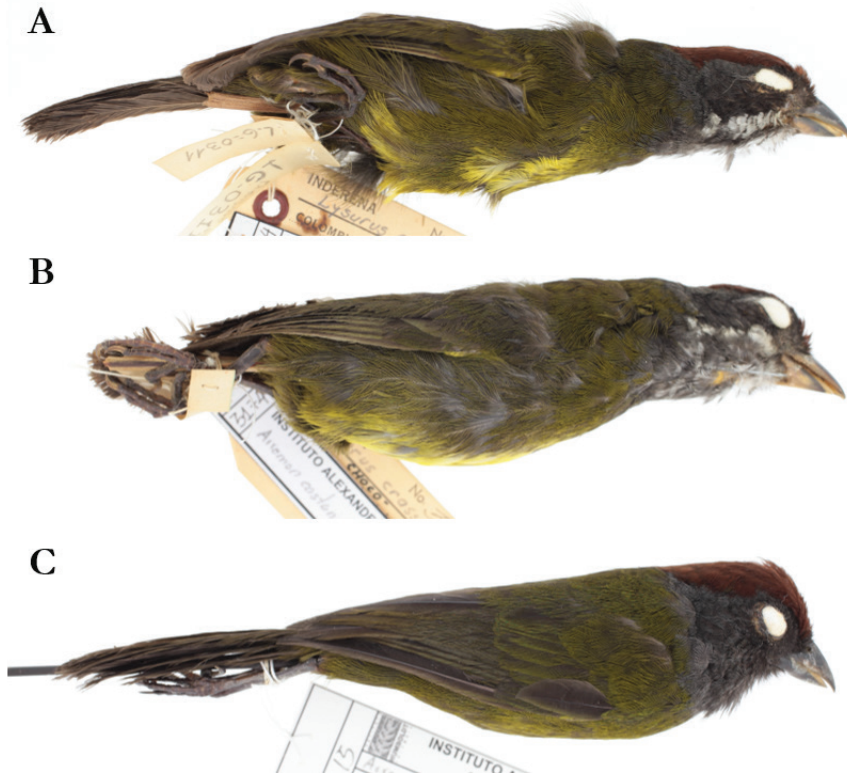


Figure 7. Lateral views of specimens of Sooty-faced Finch *A. crassirostris* (A–B) collected on the Colombian slope of Cerro Tacarcuna, compared to a specimen of Olive Finch *A. castaneiceps* (C) from the West Andes of Colombia: (A) male IAvH-A 3164 and (B) female IAvH-A 3174, from Alto Barrigonal, dpto. Chocó, Colombia; (C) male IAvH-A 8315 from Reserva Natural Río Nambí, municipality Barbacoas, dpto. Nariño, Colombia (S. Sierra)

Andes and the Chiriquí highlands, respectively, whereas the remaining species (Black-headed Antthrush and Yellow-throated Chlorospingus) occur in the foothills of adjacent ranges such as San Blas and Serranía del Baudó. These range extensions, plus another also presented here, are indicative of the poorly known avifauna of the region.

Our field work produced the first specimens of Bare-shanked Screech Owl, Violet-capped Hummingbird, Tacarcuna Tapaculo and Varied Solitaire for Colombia. Another eight records represented the first or second specimen records of subspecies endemic to the Darién highlands (e.g. *Phaethornis guy coruscans*, *Catharus f. fuscater*, *Basileuterus tristriatus tacarcunae*) and foothills (*Schiffornis veraepacis acrolophites*, *Chlorospingus flavigularis hypophaeus*). Clearly, the Darién requires further ornithological work to improve our taxonomic, geographic and temporal representation of several poorly known species in bird collections (Cuervo *et al.* 2008). Sound-recording also yielded the first record of Tacarcuna Tapaculo song, and documented the vocalisations on the Colombian side of endemic taxa such as Bare-shanked Screech Owl, Ochraceous Wren, Varied Solitaire and Tacarcuna Chlorospingus.

Our preliminary list includes 84 species from the cloud forest belt at 900–1,150 m. Although this inventory is probably far from complete, the combination of visual and aural observations, supplemented by sound-recordings and mist-netting enabled us to assemble a representative inventory swiftly. These complementary methodologies have

been recommended as the most appropriate for rapid and efficient inventories of tropical forests (Parker 1991, Salaman & Donegan 1998, Stiles & Bohórquez 2000). More species will be added as further field work is conducted and higher elevations are explored in the Tacarcuna range. For example, Robbins *et al.* (1985) recorded 186 species on Cerro Pirre at 1,000–1,500 m, although species richness (244) was concentrated in the foothills (600–1,000 m).

Nearby lowland ecosystems are currently protected in Colombia within Los Katíos National Park, which covers 72,000 ha at 50–600 m, with 412 bird species recorded (Rodríguez 1982). This park is connected to Darién National Park in Panama (579,000 ha). Highland and lowland Darién endemics are of conservation concern, especially because eight species are currently considered nationally threatened in Colombia (Renjifo *et al.* 2002). Moreover, the elevational distribution of most Darién endemics is concentrated above 600 m, based on the midpoints of each species' range (Fig. 8A). Exceptions are the rare Spiny-faced Antshrike *Xenornis setifrons* and Yellow-green Tyrannulet *Phylloscartes flavovirens*. For highland species, 15 of 16 reach their lower elevational limit at or above 600 m, whereas foothill species attain their upper elevational limit above 600 m. This elevational distribution shown by the endemic avifauna of Darién draws attention to the need to protect the highlands, especially in Colombia where Los Katíos National Park covers forests only below 600 m.

To conserve species endemic to the Darién highlands, one option would be to extend Los Katíos National Park through the Serranía del Darién to the Panamanian border. However, we suggest that a conservation unit, besides including the Serranía del Darién, also should cover the better-preserved Central and Pacific serranías of Pirre and Jungurudó, and the adjacent massifs (Cerro Quía, Alturas de Nique, Altos de Aspavé, Cordillera de Juradó). These mountains harbour six endemics not known to occur in the Serranía del Darién, which has ten endemics confined to it (Fig. 8A). Protecting this area will also conserve high endemism at the subspecies level as the Darién avifauna includes at least 24 endemic subspecies, 21 of them mainly found above 600 m (Fig. 8B). However, endemism could be higher because this region is the contact zone for three well-differentiated lowland faunas, the Pacific coast, Darién and Sinú regions (Haffer 1959), and several endemic subspecies

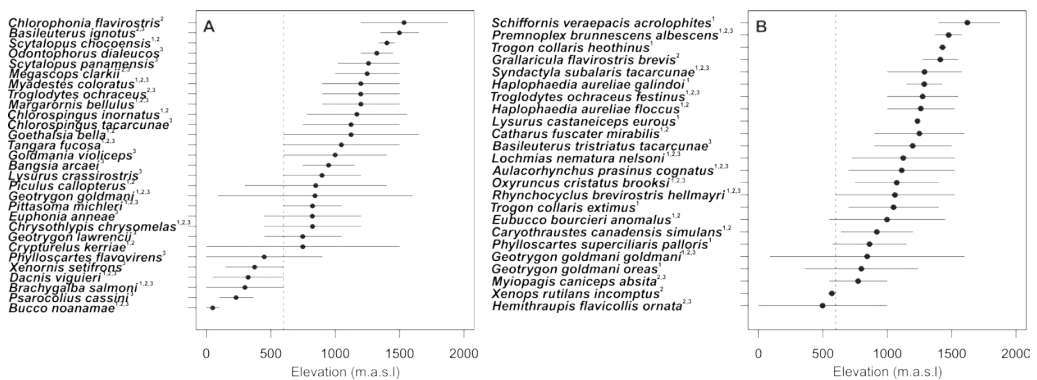


Figure 8. Elevational and geographic distribution of 29 restricted-range species (A) and 24 restricted-range subspecies (B) in the Darién lowlands and highlands. Taxa ranges (horizontal bars) are ordered according to their elevational midpoint (black dots). Note that most taxon ranges are concentrated above 600 m as shown by the vertical dashed line. Taxon names are followed by one or more superscripts indicating geographic distribution. ¹Pacific: Serranía de Jungurudó, Cerro Sapo and Serranía de Majé. ²Central: Serranía de Pirre, Cerro Quía and Alturas de Nique. ³Caribbean: Serranía del Darién including Cerro Tacarcuna and Cerro Malí. Data from Wetmore (1965, 1968, 1973), Wetmore *et al.* (1984), Robbins *et al.* (1985), Hilty & Brown (1986), Ridgely & Gwynne (1989), Pearman (1993), Angehr & Christian (2000) and Angehr *et al.* (2004).

could potentially represent distinctive species (e.g. *Basileuterus tristriatus tacarcunae*; Donegan 2014). Finally, protection of the Darién could guarantee the conservation of one of the major congregatory zones for Nearctic migratory birds in the Americas (Bayly *et al.* 2014).

Currently, the main threats to the Darién lowland and highland ecosystems are habitat loss and fragmentation due to cattle ranching and large-scale agriculture (e.g. banana plantations), which have accelerated in recent decades in Panama and Colombia (Rangel-C. 2004, Angehr *et al.* 2004, Sánchez-Cuervo & Aide 2013). Moreover, critical habitats for threatened species such as the Darién highlands could be especially vulnerable to climate change because of the small ranges and isolation of their endemic populations. Indeed, most of those species whose 'climate envelope' is projected to disappear in Colombia due to climate change are confined to isolated mountains or regions with well-defined geographic barriers. For example, in the Darién, optimal habitat for Violet-capped Hummingbird is projected to disappear by 2050 (Velásquez-Tibatá *et al.* 2013). We hope that this study will encourage further biological exploration of the region, and more importantly, draw the attention of environmental agencies and local conservationists as to the need for effective monitoring and implementation of conservation action in the Colombian Darién. Establishing a large bi-national protected area would represent a significant step towards the preservation of one of the most interesting biogeographical regions in the Neotropics (Haffer 1970).

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- Addresses:* Luis Miguel Renjifo, Depto. de Ecología y Territorio, Facultad de Estudios Ambientales y Rurales, Pontificia Universidad Javeriana, Bogotá, Colombia, e-mail: lmrenjifo@javeriana.edu.co. Augusto Repizo, Profesional de Apoyo, Parque Nacional Natural El Tuparro, Vichada, Colombia, e-mail: augustorepizo@gmail.com. Juan Miguel Ruiz-Ovalle, Fundación Ecotrópico, Calle 127C #5A-74, Bogotá, Colombia, e-mail: susande.juanmiguel@gmail.com. Sergio Ocampo, Fundación Ecológica Gabriel Arango Restrepo, Calle 66 #23B-10, Manizales, Colombia, e-mail: sergiofundegar@gmail.com. Jorge Enrique Avendaño, Laboratorio de Biología Evolutiva de Vertebrados, Universidad de los Andes, Bogotá, Colombia, e-mail: jorgeavec@gmail.com

Appendix 1

Birds recorded in the Cerro Tacarcuna foothills (450–900 m) and at our study site (900–1,150 m) on 4–7 August 2010. Types of record: V = visual, A = aural, T = sound-recorded, C = trapped, S = specimen. No. of individuals captured in parenthesis. *Colombian near-endemic (Chaparro *et al.* 2013). Taxonomy follows Remsen *et al.* (2016).

Family / English name	Scientific name	Foothills	Study site
TINAMIDAE			
Little Tinamou	<i>Crypturellus soui</i>	A	
CRACIDAE			
Crested Guan	<i>Penelope purpurascens</i>		V
Great Curassow	<i>Crax rubra</i>	V	
ODONTOPHORIDAE			
Tawny-faced Quail	<i>Rhynchortyx cinctus</i>	S	

Family / English name	Scientific name	Foothills	Study site
ACCIPITRIDAE			
Barred Hawk	<i>Morphnarchus princeps</i>		VA
Black Hawk-Eagle	<i>Spizaetus tyrannus</i>	A	A
White Hawk	<i>Pseudastur cf. albicollis</i>		V
COLUMBIDAE			
Short-billed Pigeon	<i>Patagioenas nigrirostris</i>		A
Russet-crowned Quail-Dove	<i>Geotrygon goldmani*</i>		AT
Violaceous Quail-Dove	<i>Geotrygon violacea</i>		VAT
CUCULIDAE			
Squirrel Cuckoo	<i>Piaya cayana</i>		A
STRIGIDAE			
Bare-shanked Screech Owl	<i>Megascops clarkii</i>		VATS
Mottled Owl	<i>Ciccaba virgata</i>		AT
TROCHILIDAE			
White-tipped Sicklebill	<i>Eutoxeres aquila</i>		C (1)
Stripe-throated Hermit	<i>Phaethornis striigularis</i>		V
Green Hermit	<i>Phaethornis guy</i>		VCS (3)
Tooth-billed Hummingbird	<i>Androdon aequatorialis*</i>		C (3)
Greenish Puffleg	<i>Haplophoedia aureliae*</i>		CS (2)
Green-crowned Brilliant	<i>Heliodoxa jacula</i>		C (1)
Bronze-tailed Plumeleteer	<i>Chalybura urochrysis</i>		C (2)
Crowned Woodnymph	<i>Thalurania colombica</i>	V	
Rufous-tailed Hummingbird	<i>Amazilia tzacatl</i>		
Violet-capped Hummingbird	<i>Goldmania violiceps</i>		CS (2)
TROGONIDAE			
Slaty-tailed Trogon	<i>Trogon massena</i>		AT
Black-throated Trogon	<i>Trogon rufus</i>		A
MOMOTIDAE			
Broad-billed Motmot	<i>Electron platyrhynchum</i>	VA	
Rufous-capped Motmot	<i>Baryphthengus ruficapillus</i>		A
CAPITONIDAE			
Red-headed Barbet	<i>Eubucco bourcierii</i>		V
RAMPHASTIDAE			
Black-mandibled Toucan	<i>Ramphastos ambiguus</i>		VAT
Emerald Toucanet	<i>Aulacorhynchus prasinus</i>		VA
PICIDAE			
Olivaceous Piculet	<i>Picumnus olivaceus</i>	A	
Smoky-brown Woodpecker	<i>Picoides fumigatus</i>		VA
PSITTACIDAE			
Saffron-headed Parrot	<i>Pyrilia pyrilia*</i>		A
Mealy Parrot	<i>Amazona farinosa</i>		AT
Red-and-green Macaw	<i>Ara chloropterus</i>		A
THAMNOPHILIDAE			
Black-crowned Antshrike	<i>Thamnophilus atrinucha</i>	A	VA
Plain Antvireo	<i>Dysithamnus mentalis</i>		VATC (1)
Spot-crowned Antvireo	<i>Dysithamnus puncticeps</i>		V
Slaty Antwren	<i>Myrmotherula schisticolor</i>		VA
Chestnut-backed Antbird	<i>Poliocrania exsul</i>		VA
Zeledon's Antbird	<i>Hafferia zeledoni</i>		VAT
Bicoloured Antbird	<i>Gymnopithys bicolor</i>		VAT (1)

Family / English name	Scientific name	Foothills	Study site
Ocellated Antbird	<i>Phaenostictus mcleannani</i>		VAT
RHINOCRYPTIDAE			
Tacarcuna Tapaculo	<i>Scytalopus panamensis*</i>		VATS
FORMICARIIDAE			
Black-faced Antthrush	<i>Formicarius analis</i>	A	
Black-headed Antthrush	<i>Formicarius nigricapillus</i>		VAT
FURNARIIDAE			
Olivaceous Woodcreeper	<i>Sittasomus griseicapillus</i>		V
Long-tailed Woodcreeper	<i>Deconychura longicauda</i>		V
Plain-brown Woodcreeper	<i>Dendrocincla fuliginosa</i>		VAT
Wedge-billed Woodcreeper	<i>Glyphorhynchus spirurus</i>		VC (1)
Spotted Woodcreeper	<i>Xiphorhynchus erythropygius</i>		VAT
Brown-billed Scythebill	<i>Campylorhamphus pusillus</i>		VAT
Streak-headed Woodcreeper	<i>Lepidocolaptes souleyetii</i>		A
Plain Xenops	<i>Xenops minutus</i>		V
Scaly-throated Foliage-gleaner	<i>Anabacerthia variegaticeps</i>		V
Lineated Foliage-gleaner	<i>Syndactyla subalaris</i>		VAT
Beautiful Treerunner	<i>Margarornis bellulus*</i>		V
Red-faced Spinetail	<i>Cranioleuca erythroptus</i>		V
TYRANNIDAE			
Rufous-browed Tyrannulet	<i>Phylloscartes superciliaris</i>		V
Olive-striped Flycatcher	<i>Mionectes olivaceus</i>		AC (3)
Scale-crested Pygmy Tyrant	<i>Lophotriccus pileatus</i>		VAT
White-throated Spadebill	<i>Platyrinchus mystaceus</i>		VATC (1)
Smoke-coloured Pewee	<i>Contopus fumigatus</i>		A
Tufted Flycatcher	<i>Mitrephanes phaeocercus</i>		VATS
Dusky-capped Flycatcher	<i>Myiarchus tuberculifer</i>		AV
PIPRIDAE			
White-bibbed Manakin	<i>Corapipo leucorrhoa*</i>		VAC (10)
Green Manakin	<i>Cryptopipo holochlora</i>		VC (1)
TITYRIDAE			
Russet-winged Schiffornis	<i>Schiffornis stenorhyncha*</i>		VACS (1)
TROGLODYTIDAE			
Scaly-breasted Wren	<i>Microcerculus marginatus</i>	A	A
Ochraceous Wren	<i>Troglodytes ochraceus</i>		VAT
White-headed Wren	<i>Campylorhynchus albobrunneus*</i>		VA
Sooty-headed Wren	<i>Pheugopedius spadix*</i>		VA
White-breasted Wood Wren	<i>Henicorhina leucosticta</i>	A	
Grey-breasted Wood Wren	<i>Henicorhina leucophrys</i>		VAT
Song Wren	<i>Cyphorhinus cf. phaeocephalus</i>		A
TURDIDAE			
Varied Solitaire	<i>Myadestes coloratus</i>		VATCS
Slaty-backed Nightingale-Thrush	<i>Catharus fuscater</i>		VACS
THRAUPIDAE			
Blue-and-gold Tanager	<i>Bangsia arcaei</i>		V
Speckled Tanager	<i>Tangara guttata</i>		V
Green-naped Tanager	<i>Tangara fucosa</i>		V
Bay-headed Tanager	<i>Tangara gyrola</i>		V
Emerald Tanager	<i>Tangara florida</i>		V
Silver-throated Tanager	<i>Tangara icterocephala</i>		V

Family / English name	Scientific name	Foothills	Study site
Black-and-yellow Tanager	<i>Chrysothlypis chrysomelas</i>		V
Bananaquit	<i>Coereba flaveola</i>		C (1)
EMBERIZIDAE			
Tacarcuna Chlorospingus	<i>Chlorospingus tacarcunae</i>		VAT
Yellow-throated Chlorospingus	<i>Chlorospingus flavigularis</i>		VATC (2)
Chestnut-capped Brush Finch	<i>Arremon brunneinucha</i>		VAC (3)
CARDINALIDAE			
Hepatic Tanager	<i>Piranga flava</i>		V
PARULIDAE			
Buff-rumped Warbler	<i>Myiothlypis fulvicauda</i>		VA
Three-striped Warbler	<i>Basileuterus tristriatus</i>		VACS (1)
Slate-throated Redstart	<i>Myioborus miniatus</i>		VAT
FRINGILLIDAE			
Tawny-capped Euphonia	<i>Euphonia annae</i>		VAC (1)

Appendix 2

Sound-recordings used in vocal comparisons of *Scytalopus* tapaculos (see text). Sound collections: BSA = Colección de Sonidos Animales of Instituto Alexander von Humboldt; XC = xeno-canto.org; ML = Macaulay Library. Songs: Tacarcuna Tapaculo *S. panamensis* (XC184864, XC184866, XC184868); Chocó Tapaculo *S. chocoensis* (XC119663, XC85493, XC60679); Nariño Tapaculo *S. viciniior* (XC58880, XC82587, BSA 15041). Calls: *S. panamensis* (XC184857-58, XC184860); *S. chocoensis* (ML 25770, ML 25839, ML 25843, ML 60326, XC8049, BSA 11716); *S. viciniior* (XC51263, XC89856, XC102391, XC121576, XC128511, BSA 19470, BSA 30763).