

Vocal and plumage differentiation of Perijá Brush-Finch *Atlapetes (latinuchus) nigrifrons* and Mérida Brush-Finch *Atlapetes (albofrenatus) meridae* from putative related or conspecific taxa

Diferenciación en vocalizaciones y plumajes de Atlapetes (latinuchus) nigrifrons y Atlapetes (albofrenatus) meridae de taxones considerados como relacionados o co-específicos

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Abstract

We present the first published sound recordings and photographs of live individuals of the Perijá Brush-Finch *Atlapetes nigrifrons*. Studies of plumages support conclusions of previous studies that this species only superficially resembles Yellow-breasted Brush-Finch *A. latinuchus* (with which it is often lumped on the basis of its grey mantle and yellow breast). Instead, it shares several plumage features with Santa Marta Brush-Finch *A. melanocephalus* and Moustached Brush-Finch *A. albofrenatus*, including a more extensively black head and greyish cheek patches. Perijá Brush-Finch has a distinct and uniquely varied vocal repertoire, involving: (i) a slow-whistled song (as found in *A. latinuchus*, *A. melanocephalus* and rarely in nominate *A. albofrenatus*), (ii) a cascading call (as found in *A. melanocephalus* and *A. albofrenatus*); (iii) a series of trills of increasing speed (as found only in *A. albofrenatus*); and (iv) shorter calls. The vocalizations of *A. nigrifrons* differ qualitatively from each putative related taxon in note shape (except for "series of trills" and nominate *albofrenatus*). Subspecies *meridae* of *A. albofrenatus* is distinct from both *A. albofrenatus* and *A. nigrifrons* in its principal "series of trills" song and also has a distinct vocal repertoire, meaning that it can also be recommended for species rank. Also, when *nigrifrons* is removed, *A. latinuchus* has a consistent vocal repertoire across all its range. Finally, differentiation in slow-whistled songs is evident between various groups of *A. latinuchus*, but molecular studies and a greater vocal sample should be considered before making further taxonomic changes in this group.

Keywords Taxonomy, vocalizations, oscine, *Atlapetes*.

Resumen

Presentamos las primeras grabaciones y fotografías *in vivo* de *Atlapetes nigrifrons*. Estudios de plumajes apoyan los resultados de investigaciones anteriores, las cuales han concluido que esta especie se parece superficialmente a *A. latinuchus* (de la cual se considera frecuentemente como subespecie debido a su espalda gris y pecho amarillo). No obstante, comparte varios aspectos de su plumaje con *A. melanocephalus* y *A. albofrenatus* como son la mayor presencia de negro en su cabeza y gris en las mejillas. *A. nigrifrons* tiene un repertorio vocal distinto y variable, constituido por: (i) un canto de silbidos lentos (como en *A. latinuchus* y *A. melanocephalus* y escasamente en la subespecie nominal de *A. albofrenatus*), (ii) un reclamo estridente de interacción (como en *A. melanocephalus* y *A. albofrenatus*); (iii) series de trillizos incrementándose cada vez en velocidad (como únicamente en *A. albofrenatus*) y (iv) reclamos cortos. Las vocalizaciones de *A. nigrifrons* difieren cualitativamente de cada una de las otras especies relacionadas en la forma de las notas (excepto los trillizos y la subespecie nominal de *albofrenatus*). La subespecie *meridae* de *A. albofrenatus* difiere en su vocalización principal (el trillizo) de los demás taxones y también tiene un repertorio vocal diferente, por lo cual se recomienda tratarla también como una especie separada. Además, cuando se quita *nigrifrons*, *A. latinuchus* tiene un repertorio vocal consistente a través de toda su distribución. Finalmente, la diferenciación en los cantos de silbidos, es evidente entre diferentes poblaciones de *A. latinuchus*; sin embargo, se recomiendan estudios con más grabaciones y análisis moleculares antes de realizar otros cambios a la taxonomía del grupo.

Parabras claves Taxonomía, vocalizaciones, oscine, *Atlapetes*.

Introduction

Yellow-breasted brush-finches occurring in the Perijá range are widely treated as a separate species Perijá

Brush-Finch *A. nigrifrons*, particularly in publications concerning Colombian birds (e.g. Salaman *et al.* 2008, 2010, McMullan *et al.* 2010, 2011, Olaciregui & Botero-Delgado 2012, McMullan & Donegan 2014), following

Donegan & Huertas (2006). However, others (e.g. Gill & Wright 2006, Rising *et al.* 2011, Gill & Donkser 2014, Remsen *et al.* 2014, Dickinson & Christidis 2014) have continued to follow historical treatments (Meyer de Schauensee 1966, Hilty & Brown 1986, Paynter 1978, Remsen & Graves 1995, García-Moreno & Fjeldså 1999, Dickinson 2003) in lumping the taxon with apparently unrelated Yellow-breasted Brush-Finch *A. latinuchus*. This differing treatment in the literature results from negative commentary and scepticism towards Donegan & Huertas (2006)'s proposals by several contributors to Remsen *et al.* (2014), who doubted the morphological data supporting the split and wished to see additional published molecular and/or vocal data before considering further taxonomic changes to this group.

The Serranía de Perijá was first subject to ornithological study on the Venezuelan side by Osgood & Conover (1922) and later in greater detail by various expeditions led and directed by the Phelps family (summarised in Paynter 1982; see further e.g. Phelps & Gilliard 1940; Phelps 1944; Phelps & Phelps 1952, 1953; Avelado & Ginés 1952) resulting in the description of tens of endemic montane subspecies. Perijá Brush-Finch *Atlapetes (latinuchus) nigrifrons* Phelps & Gilliard, 1940 is one such endemic. On the Colombian side, the range has been subject to remarkably few historical collections and little fieldwork until recently. M. A. Carriker Jr. collected at various sites during March – July 1942 (summarised in Paynter & Traylor 1981). These and other studies revealed the Serranía de Perijá to have several distinct elements in its avifauna. Perijá Thistletail *Schizoeaca perijana* and Perijá Metaltail *Metallura iracunda* were, for years, the only presently recognised endemics (Stattersfield *et al.* 1998), with Phelps' Brush-Finch *Arremon perijana* more recently recognised at this rank (Cadena & Cuervo 2009).

Studies of the Perijá mountains embracing their full elevational range on the Colombian side have been deterred by the security situation. Brief studies were conducted by Johnson during 1972 (Hilty & Brown 1986, p. 666). Also, the highest elevations at Cerro Pintado were subject to observations (Pearman 1993, Franco & Bravo 2005) and in the 1990s, Alejandro Camero made collections above La Jagua de Ibirico in northern Perijá. In the 2000s, the largely deforested southernmost foothills of the range near Ocaña were studied (Donegan *et al.* 2003a,b, Laverde & Stiles 2007), leading to the establishment of a ProAves nature reserve in the region, RNA Hormiguero de Tocorcoma. However, further explorations did not take place following the notorious kidnapping of an ornithologist on the Colombian side of Perijá (Malakoff 2004) and the abandonment of another expedition following a security incident (Fundación ProAves de Colombia 2006). The security situation

resulted in many species of the region being known only from museum drawers, complicating taxonomic studies for the many Andean birds with distinctive Perijá 'subspecies'.

In the absence of vocal data for *nigrifrons* and several other taxa, in order to assess the rank of then new taxon *yariguierum*, Donegan & Huertas (2006) conducted a cladistic study of north Andean *Atlapetes* using morphological characters. This study supported describing *yariguierum* as a subspecies of *latinuchus*, but highlighted the position of *nigrifrons* as "a clear anomaly in the current sequence" when treated as a subspecies of *latinuchus*. Donegan & Huertas (2006) considered *nigrifrons* likely to be closer related to each of the Santa Marta Brush-Finch *A. melanocephalus*, Moustached Brush-Finch *A. albofrenatus* and a potentially undescribed taxon referred to as the "Perijá bird" (discussed further below) than to *A. latinuchus*. Paynter (1978) had previously drawn attention to the morphological similarity of *A. l. nigrifrons* (then *A. l. phelpsi*) and *A. melanocephalus*, which share a black forehead (with *A. melanocephalus* possessing an entirely black crown), black chin, lack of pale moustachial markings (the malar merging with the mask), distinctly greyish cheeks and a paler grey back, features not found in northern *A. latinuchus* taxa. Donegan & Huertas (2006) concluded that "assignment of *A. l. nigrifrons* to the *A. latinuchus* species-group appears to be a clear example of the current sequence failing to reflect natural groupings", a proposition previously mooted for some (unspecified) northern *Atlapetes* by García-Moreno & Fjeldså (1999). They recommended that *A. nigrifrons* be afforded species rank, on account of it neither being related to *latinuchus* nor morphologically similar to other described species. Donegan & Huertas (2006) also found no support for a relationship between the two described *A. albofrenatus* subspecies, namely the nominate form of the East Andes and *meridae* of the Venezuelan Andes.

Donegan & Huertas (2006) also drew attention to a previously undescribed morphotype referred to as the "Perijá bird". This was treated as an undescribed subspecies of Moustached Brush-Finch *A. albofrenatus* by McMullan *et al.* (2010, 2011) and illustrated as such in McMullan & Donegan (2014). Two individuals of this morphotype were recorded by Alejandro Camero & Arturo Rodriguez at elevations (1,400-1,500 m) locally below habitats supporting *A. nigrifrons* in La Jagua de Ibirico municipality, northern Perijá range. One of these specimens was collected (Figs. 7-8). Intermediates between the Perijá bird morphotype and nominate *A. albofrenatus* are represented by various specimens collected in Norte de Santander (e.g. Fig. 9, showing specimens at Museum of Zoology University of Michigan - MZUM; and also a longer series at the Academy of

National Sciences, Philadelphia - ANSP), none of which include grey-backed birds. Birds of similar intermediate morphotypes have been observed, photographed and sound recorded (Fig. 12C-D) during recent fieldwork at RNA Hormiguero de Tocorcoma, Norte de Santander (L. E. Urueña *in litt.*, F. Lambert *in litt.*). Again, both 'pure' nominate *albofrenatus* and intermediates are present at this locality, but no grey-backed birds have ever been observed.

More recently, the molecular biology of northern *Atlapetes* has been studied as part of a broader study of Emberizidae (Klicka *et al.* 2014). Santa Marta Brush-Finch *A. melanocephalus* and Moustached Brush-Finch *A. albofrenatus* formed a well-supported group, together with Ochre-breasted Brush-Finch *A. semirufus*. This group was not found to be very closely related to the *A. latinuchus* clade. The molecular study had relatively good taxon sampling to species level but did not include *nigrifrons*.

With the improving security situation on the Colombian side of the Perijá range, recent fieldwork has now taken place. In this paper, we publish results and materials related to *Atlapetes nigrifrons*, including the first published sound recordings and photographs of live birds in the field. We compare plumages and vocalizations of this and other putative related brush-finch taxa to assess their taxonomic rank. Studies of voice are lacking for northern *Atlapetes* and may be of assistance in addressing current controversies over species limits. Whilst voice has been widely used to delimit species in suboscine passerines (in which vocalizations are considered innate: Kroodsma 1984, Isler *et al.* 1998), vocal characters have been less-frequently studied in Neotropical oscines. Gape muscle strength and bill mass must however influence the vocal repertoire of oscines, e.g. their ability to trill at given speeds or deliver notes of certain lengths or frequencies (e.g. Podos *et al.* 2004), and vocal differentiation is considered relevant to species limits in all birds (e.g. Helbig *et al.* 2002, Tobias *et al.* 2010). Vocal differences are evident between allopatric oscine populations (e.g. Cadena *et al.* 2007, Donegan & Avendaño 2010) and differences in vocal repertoire and structure in another American nine-primaried oscine genus (*Basileuterus*) track molecular differentiation (Donegan 2014).

Methods

With the improving security situation in Colombia, from around 2009, Alex Cortés, Juan Pablo López and others carried out various studies to find a possible site for ornithological study and conservation in the Perijá range. Further to this, Fundación ProAves with the support of Rainforest Trust and other partners, acquired almost a dozen private properties in 2013 to establish the Reserva Natural de Aves 'Chamicero de Perijá' as a first protected area on the Colombian (western) side of Serranía de

Perijá. Although we understand that there has been a recent bird collecting expedition to the region, the results were unavailable to Fundación ProAves. As a result, in July 2014, PS, TE, AQ and Luis Felipe Barrera carried out bird surveys in the new reserve with a view to producing a preliminary checklist for the reserve and assessing its potential for ecotourism. The reserve and study sites are located in the Municipality of Manaure, depto. Cesar (centred around 10°22'N 72°57'W). *Atlapetes nigrifrons* was observed principally at 1,500-2,850 m, being most common at 1,700-2,400 m. The authors used observations and sound recordings to study the birds of the reserve. Data from this study were combined with TD and BH's data on other *Atlapetes* species in Santander and Antioquia (see Donegan & Huertas 2006, Donegan *et al.* 2007, 2009 for details of these studies).

We compared photographs of individuals of Perijá Brush-Finch *A. nigrifrons* taken in the field with those of other putative related species (i.e. Yellow-breasted Brush-Finch *A. latinuchus*, Santa Marta Brush-Finch *A. melanocephalus* and Moustached Brush-Finch *A. albofrenatus*) based on our fieldwork in Colombia, other available materials and museum specimens listed in Donegan & Huertas (2006). We assessed depictions of *A. nigrifrons* in leading field guides and texts based on these materials.

We studied vocalizations archived in the xeno-canto (XC) and Macaulay Library (ML) collections, as well as published recordings principally from Colombia and Venezuela (Álvarez *et al.* 2007, Boesman 2007, 2012). These comprised 40 sound recordings of nominate *A. albofrenatus*, 12 of *A. a. meridae*, 4 of *A. nigrifrons*, 74 of *A. latinuchus* (including 16 of proximate East Andes subspecies *yarigiuerum*) and 47 of *A. melanocephalus* (listed in the Appendix). Sound recordings were expanded on a desktop computer screen to show the detail visible for each individual recording in Figures 11-13 in full screen mode. We identified the kinds of vocalizations given by five brush-finch taxa: *A. latinuchus* group, *A. (l.) nigrifrons*, *A. melanocephalus*, *A. a. albofrenatus* and *A. a. meridae*. Four categories of vocalization were found in the sample. Vocalizations in recordings were assigned to one or more of them: (i) slow-whistled songs (Fig. 11); (ii) trilled songs (Fig. 12); (iii) a call termed by Hilty & Brown (1986) as a "cascading call" and by Boesman (2012) as "interaction calls" (Fig. 13), a series of repeated and rather shrill, high notes; and (iv) short calls, agitated calls given in response to playback and other contact or other vocalizations. We considered the vocal repertoire of each taxon and undertook subjective comparisons of note shape and song structure for the first three kinds of vocalizations. Short calls and other vocalizations were not compared owing to the often substantial intraspecific variation in such calls and a lack of good samples of

comparable recordings. Principal recordings were defined as those present in 50% or more of recordings. Identification of dawn songs, contact calls and other uses for vocalizations were identified based on fieldwork observations of the authors.

Results: plumages

Various photographs were taken of *A. nigrifrons* in the field (Figs. 1, 2A-B) and of specimens (Figs. 8, 9, 14). The morphological differences cited in Donegan & Huertas (2006) are supported. The distinctive identification features are its black forehead, black moustachial region concolorous with the rest of the head, rufous mid-to-rear crown and dark grey cheek patch.

Atlapetes nigrifrons differs from *A. latinuchus* (Figs. 3A-B) in having more extensive black on the head, particularly in the cheeks, moustachial, chin and forehead. Its mantle is paler than in *latinuchus*, contrasting with the black head (Figs. 1, 2C). In the most proximate subspecies, *A. latinuchus yariguierum*, the dark mantle is virtually concolorous with the black head in adult plumage

(Fig. 3A). The rufous crown of *nigrifrons* and lack of such a broad grey cheek patch distinguish it from *A. melanocephalus* (Figs. 4A-C).

Atlapetes albofrenatus was not considered closely related to *A. nigrifrons* until recently (Donegan & Huertas 2006) due to its strong moustachial, white chin and green mantle (Figs. 5-6). However, the pattern of black on the forehead and chin is similar to that of *nigrifrons* in the nominate subspecies (Fig. 5). The two described subspecies of *A. albofrenatus* differ considerably from one another in plumage also: in the extent of rufous on the crown, relative thicknesses of the black and white moustachial/malar and the presence of yellow or white on the throat (Figs. 5-6).

Juveniles of *A. nigrifrons* are undescribed. A recently collected specimen (Fig. 14) and older specimens in the Phelps collection (Fig. 10) lack a red crown (cf. *A. melanocephalus*). Juvenile specimens are very different from juveniles of *A. albofrenatus* (Fig. 14).



Figure 1. Perijá Brush-Finch *Atlapetes nigrifrons*. A. Quevedo/Fundación ProAves.

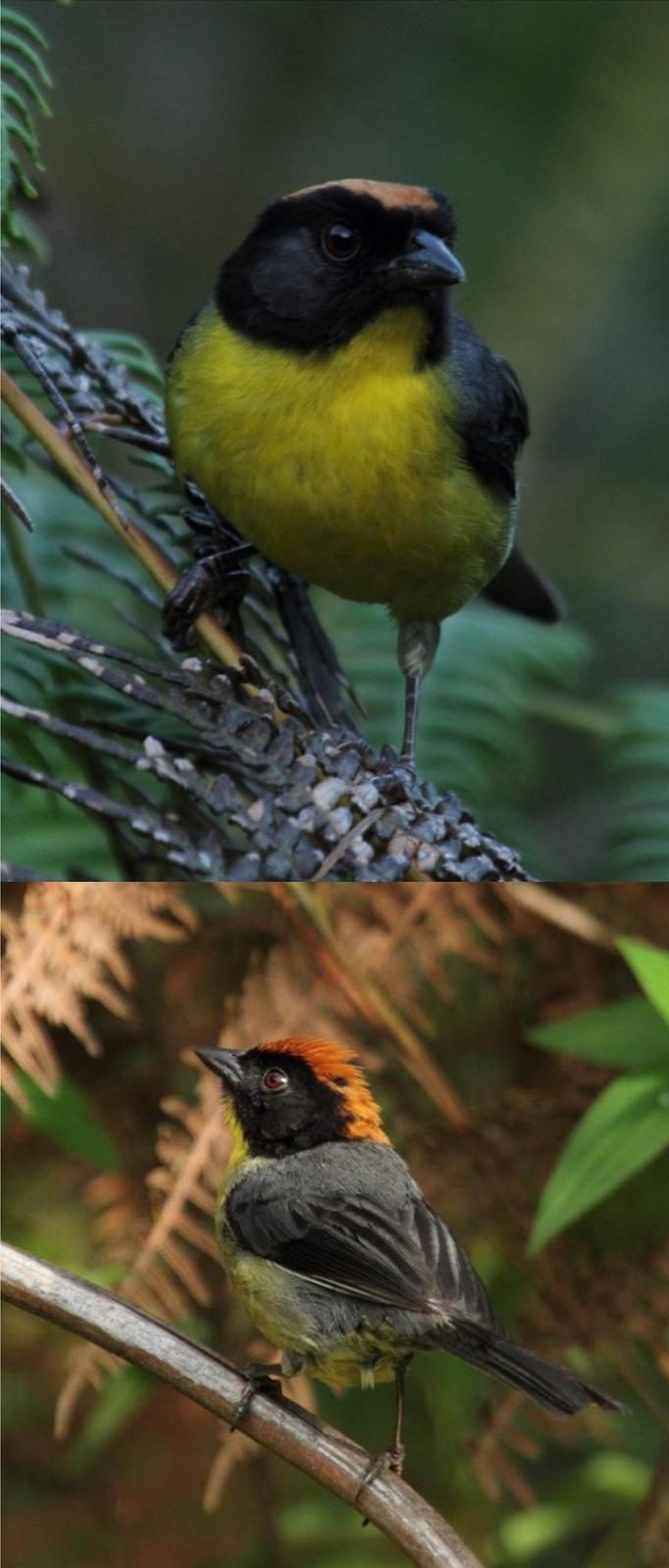


Figure 2. Perijá Brush-Finch *Atlapetes nigrifrons*.
A. Quevedo/Fundación ProAves.



Figure 3. Proximate populations of *A. latinuchus* to other taxa studied here. Above: Yellow-breasted Brush-Finch *Atlapetes latinuchus yariguierum* holotype, Alto Cantagallos, San Vicente de Chucurí, Santander, B. Huertas / Colombian EBA Project. Below. Yellow-breasted Brush-Finch *Atlapetes latinuchus elaeoprurus* of the Central Andes, La Lana, San Pedro de los Milagros, Antioquia, B. Huertas / Colombian EBA Project.



Figure 4. Santa Marta Brush-Finch *Atlapetes melanocephalus*, RNA El Dorado, Minca, Magdalena, A. Quevedo / Fundación ProAves.



Figure 5. Moustached Brush-Finch *Atlapetes albofrenatus*, T. Donegan, Agua de la Virgen, Ocaña, Norte de Santander. Intermediates between birds showing this 'typical' plumage and the 'Perijá bird' morph are also found at the same locality.



Figure 6. Mérida Brush-Finch *A. meridae*. Mérida state, Venezuela. Photograph by Anneray Westerling www.anneray-birdsite.com.

Vocalizations

Vocalizations of the taxa studied here are set out in Figures 11-13. We found slow-whistled songs to be the main vocalization type and dawn song for the *A. latinuchus* group (except *nigrifrons*). Trilled songs are the main vocalization type for the *A. albofrenatus* group. Cascading calls are typical of *A. albofrenatus* and *A. melanocephalus*.

Atlapetes nigrifrons has a uniquely extensive repertoire of vocalizations, giving each of the three kinds of main vocalization studied in detail here: slow-whistled songs (Fig. 11A-E), trilled songs (Fig. 12A-B) and cascading calls (Fig. 13A-B). The nominate subspecies of *A. albofrenatus* is closest in its vocal repertoire (Figs. 11F-G, 12C-H, 13C-D). However, slow-whistles are found in only 2 of 40 sound recordings for nominate *A. albofrenatus* and vary little in acoustic frequency compared to *A. nigrifrons*. Slow-whistle vocalizations are entirely absent from our smaller sample of *meridae* recordings, which included only trilled songs (of two kinds) (Figs. 12I-K), one cascading call (Fig. 13E) and calls.



Figure 7. the "Perijá bird" specimen, ICN 32646 collected by Alejandro Camero and Arturo Rodríguez on 9 March 1996 at vereda Alto de las Flores, La Victoria, La Jagua de Ibirico Municipality, Cesar Department, 1480m. Photograph by T. Donegan.



Figure 8. (Left to right) (i) typical nominate Moustached Brush-Finch *A. albofrenatus*; (ii) "Perijá bird" specimen; and (iii) Perijá Brush-Finch *A. nigrifrons* collected elevationally above the Perijá bird specimen at La Jagua de Ibirico, vereda El Zumbador, 1,700 m by A. Camero (ICN 32692). Photograph by T. Donegan.



Figure 9. Examples of specimens of a typical nominate Moustached Brush-Finch *A. albofrenatus* (Museum of Zoology University of Michigan no. 199329, collected 19 August 1916 by M. A. Carriker), above, and intermediate between the latter and the "Perijá bird" morphotype (Museum of Zoology University of Michigan no. 199328, collected 14 August 1916 by M. A. Carriker), both from the same locality: La Palmita, Norte de Santander. Photograph by Janet Hinshaw.



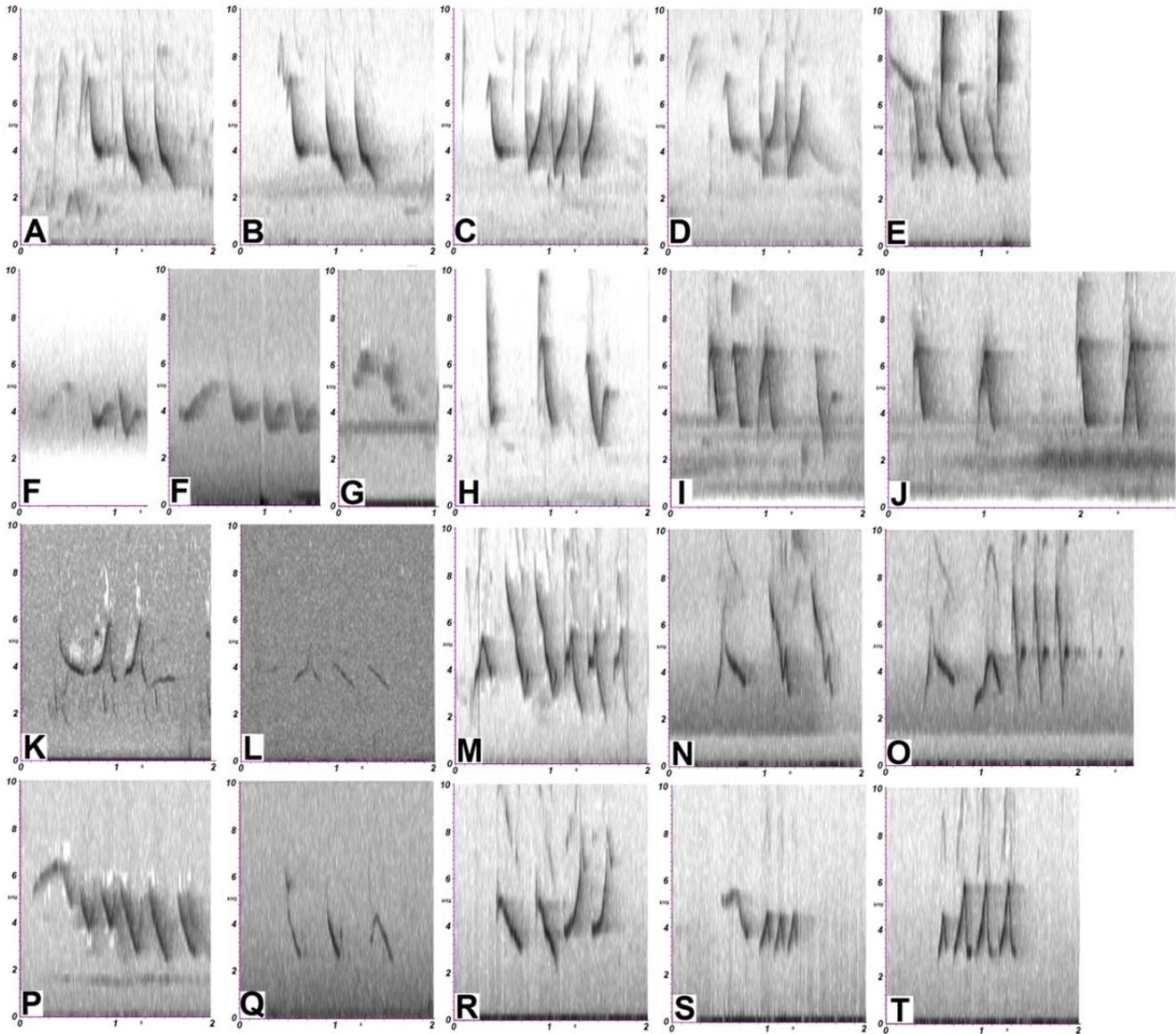


Figure 11. Slow-whistled songs of Perijá Brush-Finch *A. nigrifrons* (A-E), Moustached Brush-Finch *A. albofrenatus* (F-G), Santa Marta Brush-Finch *A. melanocephalus* (H-J), Yellow-breasted Brush-Finch *A. latinuchus yariguierum* (K-L), *A. l. elaeoprurus* (M), *A. l. cauae* (N-O), *A. l. spodionotus* (P-Q), *A. l. latinuchus /baroni* (R-T). A-D. XC203103, A. Quevedo, RNA Chamicero de Perijá, all of same individual vocalizing alone at dawn. E. XC203102, P. Salaman, RNA Chamicero de Perijá, one of three individuals vocalizing simultaneously (with calls of another bird shown at higher frequencies). F. XC45463, 56050, B. López-Lanús, Santuario de Fauna y Flora Iguaque, Villa de Leyva, Boyacá. G. Possible song (*A. albofrenatus* singing later in track not confirmed to be the same bird), XC203108, T. Donegan, Agua de la Virgen, Ocaña, Norte de Santander. H. XC165443, N. Krabbe, RNA El Dorado, Sierra Nevada de Santa Marta, Minca, Magdalena. I-J. XC10751, N. Athanas, as previous; J is part of a long series of these kinds of notes. K. XC23534, T. Donegan, Filo Pamplona, Galán, Serranía de los Yariguíes, Santander. L. XC6484, T. Donegan, Lepipuerto, El Carmen, Serranía de los Yariguíes, Santander. M. XC39533, T. Donegan, La Lana, San Pedro de los Milagros, Antioquia. N-O. XC56417, B. López-Lanús, PNN Munchique, Cauca. P. XC12705, O. Laverde, San Juan de Pasto, Daza, Nariño. Q. XC9286, A.T. Chartier, Old Chiriboga road, Pichincha, Ecuador. R-T. XC14443, R. Ahlman, ACP Abra Patricia, San Martín, Peru (identified as *latinuchus*).

Figure 10. (overleaf, bottom). The series of Perijá Brush-Finch *A. nigrifrons* at the COP collection, Venezuela. Individuals lacking a red crown on the left of the photograph are juveniles. Photograph by R. Restall.

In contrast, all non-*nigrifrons* subspecies of *A. latinuchus* whose vocalizations are known (named in Fig. 11) give only the slow-whistled song (Fig. 11K-T) among the vocalization types studied in detail here. Examples of short, very fast trills exist (e.g. XC9285), but these are rare in the sample and in Colombian populations such vocalizations do not appear to have the same territorial function as the predominant slow-whistle song. Contact calls of agitated birds, including following use of playback, can also become complex and include quick trills as elements (e.g. Álvarez *et al.* 2007, track 30). However, these have a different song structure to the deliberate trilled songs of *A. nigrifrons* or *A. albofrenatus*.

Atlapetes melanocephalus has a repertoire of slow-whistled songs (Fig. 11H-J) and cascading calls (Fig. 13F-G). However, it has not been recorded giving a vocalization equivalent to the trilled song of *A. albofrenatus* and *A. nigrifrons*.

Based on our field observations elsewhere in Colombia of subspecies *yariguierum* and *elaeoprorus*, slow-whistled songs are typically given just after dawn by these taxa. Slow-whistled songs seem to be the main territorial song for this group (and may also have the same role in *A. melanocephalus*, although the latter also gives cascading calls soon after dawn). In *A. nigrifrons* the slow-whistled song was not heard as frequently as the trilled song at dawn. However, birds would respond non-aggressively to playback of the slow-whistled song with similar vocalizations.

The slow-whistled songs of *A. nigrifrons* (Fig. 11A-E) typically start with a flowing downstroke, usually commencing with a short up-tick and decreasing in the rate of change in frequency towards the end, giving a calligraphic quality to sonograms. Various notes then follow this in combination, including slightly broken downstrokes (which also slow in rate of frequency change towards the end: Figs. 11A-B, E); and upstrokes preceded by a very fast downstroke (Fig. 11C-D). Different note shapes were observed in other species. In *A. albofrenatus*, these calls are rare and not used with any regularity as a dawn or territorial call (trilled songs instead being dawn songs). In the recording in Fig. 11G, a bird gave this call repeatedly as a contact or alarm call prior to a trilled song. These vocalizations vary little in acoustic frequency compared to the songs of *A. nigrifrons*. In *A. melanocephalus*, notes of slow-whistled songs are of a more linear shape, with sharp up and down strokes (Fig. 11H-J).

As illustrated for some subspecies by Donegan & Huertas (2006), *A. latinuchus* subspecies show considerable variation among populations in the note shape to slow-

whistled songs (Fig. 11K-T). A larger sample and better geographical sampling is now available. Note shapes of the *latinuchus* group are mostly either linear or quite complex (with multiple turning points) compared to *A. nigrifrons*. Only some of the southernmost taxa use more curved note shapes. Within *A. latinuchus*, noteworthy similarities in note shapes exist between proximate *elaeoprorus* (Fig. 11M) and *caucae* (Figs. 11N-O) which both occur in the Central and West Andes of Colombia with *elaeoprorus* further north. Subspecies *yariguierum* (East Andes, Colombia: Fig. 11K-L) has a different note shape to its slow-whistled songs. Southern populations differ further from northern Colombian groups (Figs. 11P-T). Perhaps several species are involved, but a revision of subspecies limits for this difficult complex falls outside the scope of this paper. At least, provided that *nigrifrons* is removed, the remaining *A. latinuchus* taxa have a shared vocal repertoire.

Trilled songs are absent in the sample for both *A. melanocephalus* and *A. latinuchus*. In contrast, in both subspecies of *A. albofrenatus* and *A. nigrifrons*, trilled songs are the main kind of dawn song given by individuals, presumably to mark their territories. These vocalizations are also given in response to playback in the early morning. Both subspecies of *A. albofrenatus* have a substantial repertoire of trilled songs. Typically, these are prefaced by spaced out call notes ('opening') given in fairly rhythmic repetition, followed by a series of shorter and lower notes of different note shape ('mid-section'). In some (but not all) recordings (Figs. 12C, E-I), there is then a further series of even shorter and even lower notes of yet different note shape ('ending'). Often, birds will alternate between calls including and then excluding the ending. *Atlapetes nigrifrons* vocalizes with these same two patterns (with ending: Fig. 12A; without ending: Fig. 12B).

The taxon which varies most from others in trilled songs is the Venezuelan Andes population (*meridae*) of *A. albofrenatus*. Its trilled songs are given more repeatedly (e.g. Figs. 12J-K, which represent just two samples of a typically long recording). Moreover, note shapes are usually simpler, broader in acoustic frequency bandwidth and more spaced out from one another. Most notably and in contrast to nominate *A. albofrenatus*, there is typically no "ending" section for this kind of song in *meridae*, with only one recording (<10% of sample) including such a feature (Fig. 12I). The taxon *meridae* was recently considered to meet the species ranking criteria of Tobias *et al.* (2010) based on plumages alone (N. J. Collar *in litt.* 2014). Because *meridae* is so different in its plumage (Table 1) and is considered here to be more vocally distinct in the main kind of trilled song (Fig. 12J-K) than *A. nigrifrons* is from *A. a. albofrenatus*, it is also a strong candidate for species rank.

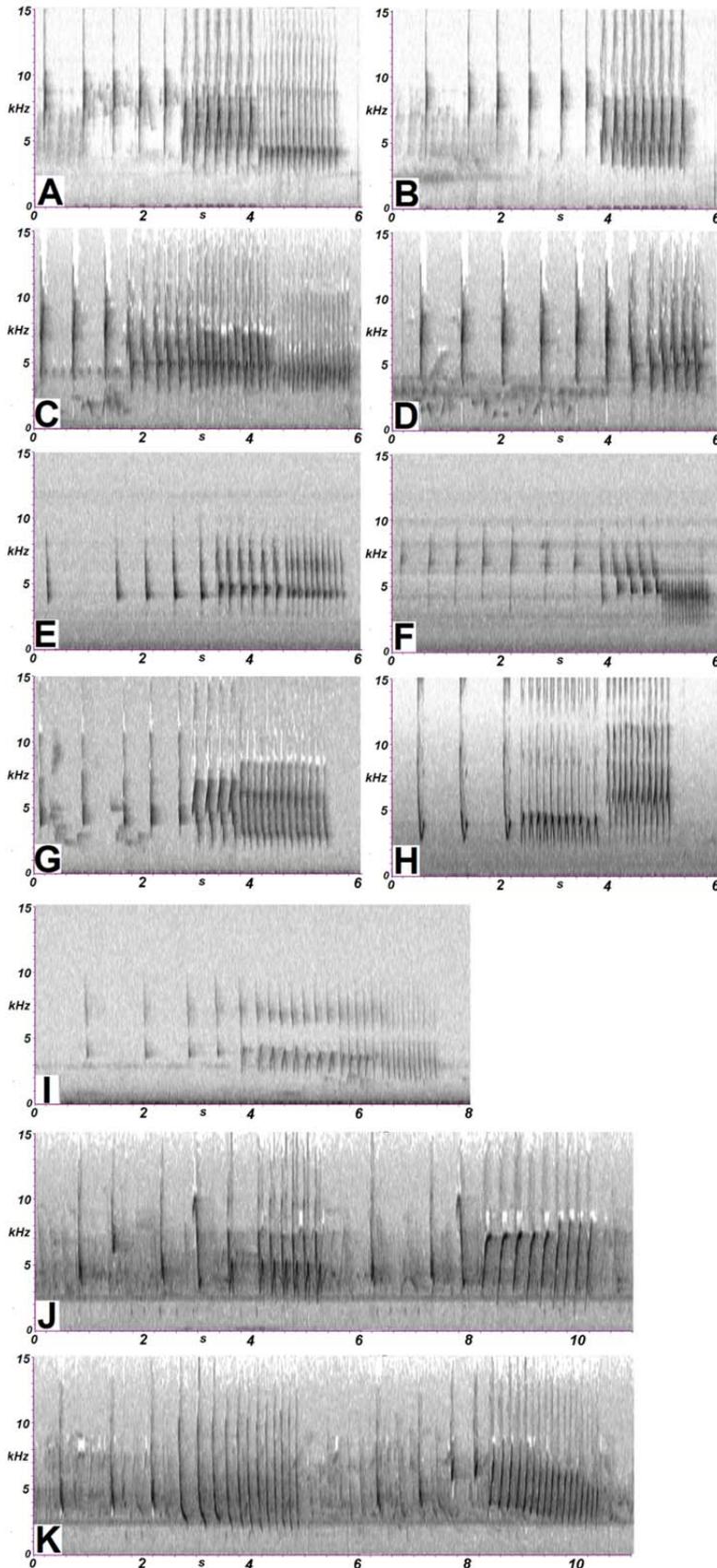


Figure 12. Trilled songs of Perijá Brush-Finch *A. nigrifrons* (A-B), Moustached Brush Finch lacking a moustache (intermediate with *A. a. subsp.* “Perijá bird” phenotype) (C-D), Moustached Brush-Finch *A. albofrenatus albofrenatus* (E-H) and Moustached Brush-Finch *A. a. meridae* (I-K). No such recordings were found for Santa Marta Brush-Finch *A. melanocephalus*. A-B. XC203104, A. Quevedo, RNA Chamicero de Perijá. C-D. XC16689, F. Lambert, RNA Hormiguero de Torcoroma, Ocaña, Norte de Santander. E. Álvarez *et al.* (2007, track 22a), J. A. López, SFF Iguaque, Villa de Leyva, Boyacá. F. Álvarez *et al.* (2007, track 22b), Agua de la Virgen, Ocaña, Norte de Santander. G. XC74417, P. Flórez, Rogitama, Arcabuco, Boyacá. H. XC84263, A. Spencer, Laguna de Pedro Palo, Cundinamarca. I. ML55732, D. Fisher, La Azulita road, near Mérida, Venezuela. J-K Boesman (2012, track 3066-1), El Morro Road, Mérida, Venezuela

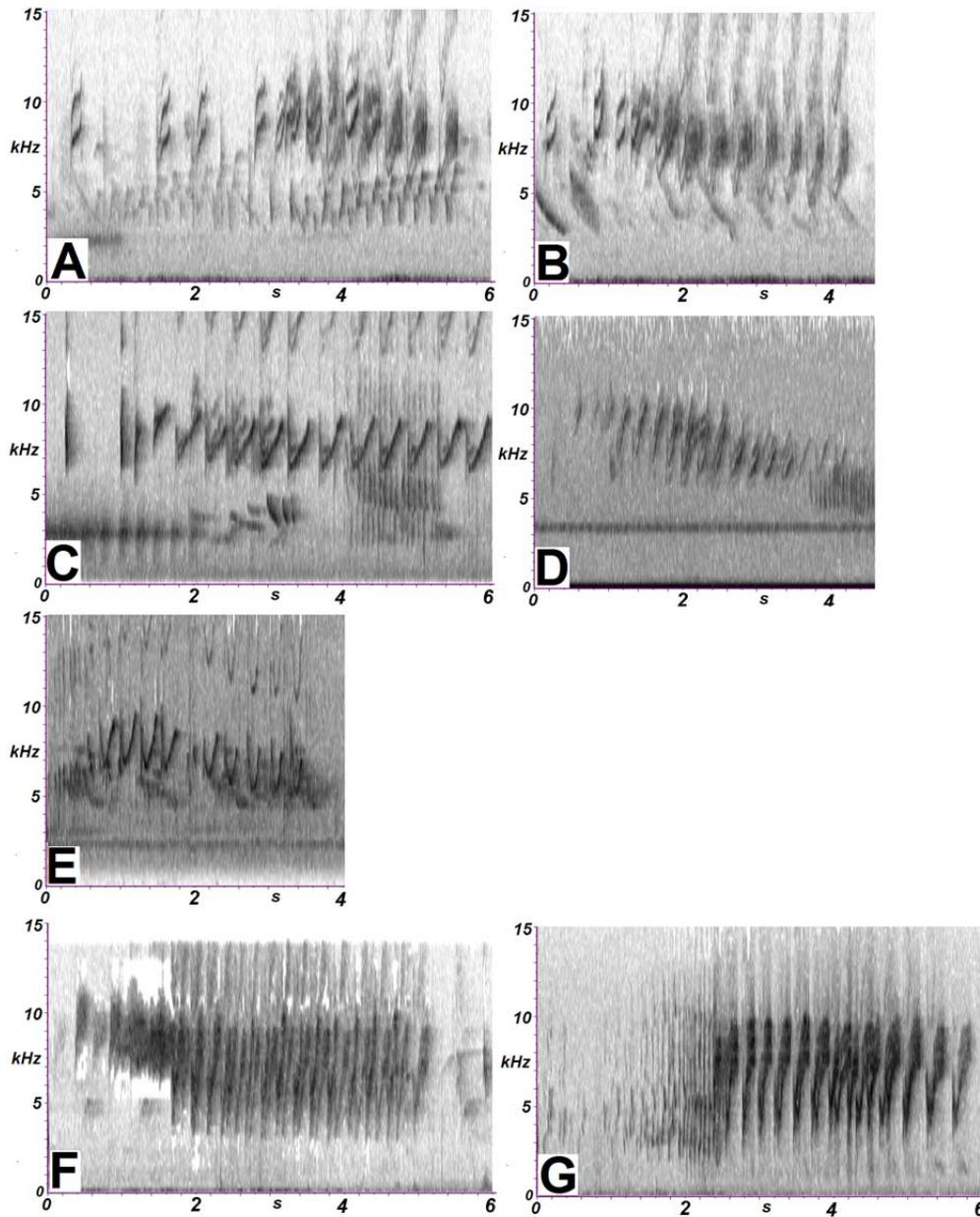


Figure 13. Cascading calls of Perijá Brush-Finch *A. nigrifrons* (A-B), nominate Moustached Brush-Finch *A. a. albofrenatus* (C-D), Moustached Brush-Finch *A. a. meridae* (E) and Santa Marta Brush-Finch *A. melanocephalus* (F-G). No such recordings were found for Yellow-breasted Brush-Finch *A. latinuchus*. A. XC203104, A. Quevedo, RNA Chamicero de Perijá, with a second individual vocalizing a different sort of call at lower acoustic frequency. B. As previous, with first two notes at lower frequencies being of Rufous-collared Sparrow *Zonotrichia capensis*. C. XC22344, A. Spencer, calls of a trio of birds, RNA Hormiguero de Torcoroma, Ocaña, Norte de Santander. D. XC44734-62650, T. Donegan, Agua de la Virgen, Ocaña, Norte de Santander. E. XC202428, H. Matheve, La Azulita, Mérida. F. XC43474, T. Donegan, RNA El Dorado, Minca, Sierra Nevada de Santa Marta, Magdalena, calls of a group. G. XC165432, N. Krabbe, as previous, duet.

The trilled songs of *A. nigrifrons* and nominate *A. albofrenatus* are similar to one another (compare Figs. 12A to 12G and 12B to 12D, for example). In nominate *A. albofrenatus*, the opening notes vary between fast upstrokes or fast downstrokes (almost straight lines on sonograms: Figs. 12C-F) and slower chips (Figs. 12G-H). The mid-section may comprise downstrokes (Fig. 12C), chips (Figs. 12E, H) or up-downstrokes of varied frequency (Fig. 12G-H). The ending is a very fast trill whose individual notes are more difficult to distinguish, but expansion of sonograms shows both downstroke-ish (Fig. 12H) and upstroke-ish (Fig. 12C) shapes.

The note shapes in trilled songs of *A. nigrifrons* are not matched equally in the *A. albofrenatus* sample, our recordings having a stronger upstroke in the mid-section than any recording of *albofrenatus* (Fig. 12A-B). However, given the considerable individual variation in the note shapes of trilled songs in *A. albofrenatus* (Fig. 12C-H), this character is unlikely to allow identification of one population from the other and is best conservatively treated as non-variable between these two taxa.

Cascading calls were found in our sample only for *A. nigrifrons* (Fig. 13A-B), *A. a. albofrenatus* (Fig. 13C-D),

A. a. meridae (Fig. 13E) and *A. melanocephalus* (Fig. 13F-G). These comprise a series of high-frequency, relatively slow-rising upstrokes, most notes being lower than previous ones and ending with more rapidly repeated or slower elements which result in a shrill or trilled quality towards the end. In all Colombian populations, it is a contact call. In *A. albofrenatus*, individual notes are simpler, thicker and more constant, with reduced trilling or wavering towards the end. In the nominate, some such songs are slower (Figs. 13C) than others (Fig. 13D); we have only a slower song in the sample for *meridae* (Fig. 13E). In *A. melanocephalus*, notes occupy a broader acoustic bandwidth (c.7-8 kHz; compared to c.4-6 kHz in *A. nigrifrons* and nominate *A. albofrenatus*).



Figure 14. Juveniles of (above) Perijá Brush-Finch *A. nigrifrons* ICN 36728, collected by A. M. Cuervo & N. Gutiérrez Pinto, dto. Cesar, mun. Manaure, abajo de vereda el Cinco, 10°21'37.7"N, 73°00'19.1"W, 1825 m, 5 July 2008; and (below) nominate Moustached Brush-Finch *A. albofrenatus* ICN 3721, Cundinamarca, Fusagasugá, Aguadita, Olivares & Bernal, 27 November 1958.

Conclusions and Discussion

The Perijá Brush-Finch *Atlapetes nigrifrons* is confirmed here to be distinctive in its plumage and has a distinct vocal repertoire from all putative related congeners and conspecifics in the *latinuchus* group. There are multiple significant plumage and vocal differences between it and each other taxon studied here (Table 1) which are similar to or exceed those between sympatric *Atlapetes* and taxa afforded species rank in this group. Vocal data support Donegan & Huertas (2006)'s separation of *A. nigrifrons* from *A. latinuchus* and their proposition that the former is more closely related to *A. melanocephalus* and *A. albofrenatus*.

The separation of *A. nigrifrons* from *A. latinuchus* seems easily justified. A more serious concern for this taxonomic revision is the relationship between *A.*

nigrifrons and *A. albofrenatus*. These two have never before been treated as conspecific, because they are so different in their morphology. Whilst they differ vocally, they show similarities in repertoire and trilled songs. It is plausible that the 'Perijá bird' specimen (and other intermediate specimens involving *A. albofrenatus* features discussed and illustrated here) might be a result of contact between *nigrifrons* and *albofrenatus*. However, the lack of any grey-mantled birds in series of intermediates (or birds observed in fieldwork in Norte de Santander where intermediates occur) and the broad consistency of plumage in collections of both *nigrifrons* (Fig. 10) and *albofrenatus* suggest otherwise. The 'Perija bird' specimen and 'pure' *nigrifrons* have been collected at proximate sites of different elevation in La Jagua de Ibirico (Fig. 8), instead suggesting elevational replacement. In our fieldwork location in Manaure, elevations of 1400-1600 m (where the 'Perijá bird' morph might be expected) were largely deforested. Overall, it seems more plausible that the 'Perijá bird' specimen represents an undescribed subspecies of northern morph of *A. albofrenatus* which intergrades with the nominate subspecies in Norte de Santander, and occurs elevationally below *A. nigrifrons* on the western slope of the Perijá mountains. However, this remains to be confirmed.

Atlapetes nigrifrons is allopatric with respect to both *A. latinuchus* and *A. melanocephalus*. Applying the biological species concept to allopatric populations involves a comparison of the differences between these and between related, sympatric species (Helbig *et al.* 2002, Remsen 2005). Two of the taxa studied here, *A. albofrenatus* and *A. latinuchus yariguierum*, are fully sympatric in the East Andes of Colombia and occur together at some localities (Donegan *et al.* 2010). They differ in vocal repertoire (not just in measurements of similar vocalizations). The differences in vocal repertoire could be thought similar in nature to those between *A. latinuchus yariguierum* and *A. nigrifrons*. Separately, Tobias *et al.* (2010) aimed to assess various sympatric bird species and considered and their differences under a scoring system, in order to produce a global standard for assessment of allopatric birds. All taxon-pairs studied in detail here score highly as against one another, greatly exceeding the recommended standard for species rank of 7 (Table 1). When a broader set of plumage, biometric and vocal characters is considered using these criteria, species rank for both *nigrifrons* and *meridae* is supported.

We therefore propose the following revised sequence for these birds:

Moustached Brush-Finch *Atlapetes albofrenatus*
(nominate subspecies, with the "Perijá bird"
morphotype, a possibly undescribed taxon of which

intermediates with *albofrenatus* exist, provisionally treated here also).

Mérida Brush-Finch *Atlapetes meridae*: monotypic.

Perijá Brush-Finch *Atlapetes nigrifrons*: monotypic.

Santa Marta Brush-Finch *Atlapetes melanocephalus*: monotypic.

Yellow-breasted Brush-Finch *Atlapetes latinuchus* (subspecies *yariguierum*, *elaeoprorus*, *caucaae*, *spodionotus*, *comptus*, *latinuchus*, *baroni* and *chugurensis*; with the rider that the validity of and limits between the last five subspecies were not considered here; and it being understood that this group is paraphyletic with respect to Pale-naped Brush-Finch *A. pallidinucha* and requires further revision: Sánchez-González *et al.* 2014).

Assessment of the morphological distinctiveness of *A. nigrifrons* by some authorities has been complicated owing to a lack of accurate plates in leading field guides and monographs. Rising *et al.* (2011) and McMullan & Donegan (2014) include broadly accurate plates. However, others in the literature suffer from inaccuracies. Hilty (2003)'s plate is reasonable, but the mantle is a little too olivaceous (not plain grey) and, whilst the black forehead is shown, the red crown stripe approaches too close to the bill and is angled towards the lores. Restall *et al.* (2006) correctly show the forehead pattern and a grey cheek patch, but the mantle is rather too dark and uncontrasting, the crown stripe is overly dark and the iris too bright. Comparisons between *A. nigrifrons* and *A. latinuchus* subspecies in this publication are further compounded due to errors in the moustachial region of other illustrated *latinuchus* taxa, which are shown blurred rather than marked with lines, or, in the case of *A. latinuchus comptus*, incorrectly merged with the black head. McMullan *et al.* (2010, 2011) incorrectly show the rufous of the crown in *nigrifrons* extending to the bill. Neither Hilty & Brown (1986), Fjeldså & Krabbe (1990) nor Ridgely & Tudor (1989, 2009) illustrate *A. nigrifrons*. It is hoped that the photographs presented here will clarify the morphology of the species for future observers and authors.

Conservation status of the Perijá Brush-Finch

Several decades of security problems in the Serranía de Perijá result from its strategic location on the Venezuelan border. Contraband, drug trafficking and cultivation are all well-known issues. It is also historically a "safe haven" for insurgents, restricting access for researchers (Malakoff 2004). However, the insurgence in some parts of the range has dissipated and safe access is now possible to such parts. The Serranía de Perijá is a mountain range with two contrasting conservation situations. Divided laterally between Colombia and Venezuela, the western

slope in Colombia has undergone massive ecological change with an estimated >95% of mature forest cover lost. What little intact forest survives is fragmented and degraded, primarily by annual dry season incendiaries that run up the steep slopes burning cattle pasturelands.

By contrast, a large proportion of the Venezuelan eastern side of Serranía de Perijá is protected by a National Park and until recently was considered relatively intact. However, recent satellite imagery and ground surveys show that the park is presently undergoing rapid changes, with colonization and associated deforestation spreading, including from over the Colombian side. Rapid deforestation in Venezuela may have been fuelled by the increased military presence in Colombia, forcing opium growers into Venezuela. This situation is compounded because historically the Sierra de Perijá National Park in Venezuela is reported to have no active management (Rodríguez & Rojas-Suárez 1995).

Of particular concern in the Serranía de Perijá are the subtropics and lower montane forests (1,700-2,400 m) where *A. nigrifrons* primarily occurs. Land at this elevation is a premium for agriculture and cattle pasture. As a consequence, there is little forest surviving at these elevations, and what is found is typically secondary forest or heavily fragmented or degraded. Observations in these fragments and secondary growth forest could reliably find pairs and small parties of *A. nigrifrons*, especially with pishing and playback, although the species was far from abundant.

The new ProAves reserve contains a relatively small population (estimated >100 individuals) but a lack of protection elsewhere in Colombia and mounting threats in Venezuela justify conservation attention on the basis of an inference of decline due to threats from narcotics cultivation, uncontrolled colonization and cattle-ranching causing the loss and fragmentation of habitat. It is therefore recommended that *Atlapetes nigrifrons* be listed on a precautionary basis as Vulnerable (VU: A2a,c; VU: B2a,b (i,iii)) with an estimated Area of Occupancy estimated to be less than 2,000 km² – most of which is on the Venezuelan side of the border.

Conservation and research actions proposed

We recommend that conservation action urgently redirects attention to the Serranía de Perijá. This species and many others (including many subspecies that warrant species-level rank) are in a dire situation. It is vital that the Sierra de Perijá National Park in Venezuela is managed and effectively protected. Conservation International-Colombia, ProAves and other entities produced a comprehensive plan in 2006 to establish a

	<i>A. albofrenatus</i>	<i>A. meridae</i>	<i>A. melanocephalus</i>	<i>A. latinuchus yariguierum</i>
Perijá Brush-Finch <i>A. nigrifrons</i>	Grey vs. green mantle (3) Presence / absence of stong grey mark on cheek (2) Absence / presence of white moustachial (3) Absence / presence of white throat (ns [2]) Acoustic frequency bandwidth of slow-whistling call (2) Tremulous ending of notes in cascading call (temporal) (3) Juvenile plumages (ns [>6]) Wing length (1) Total: 13	Grey vs. green mantle (3) Absence / presence of white moustachial (3) Presence / absence of grey mark on cheek (2) Note shape of trilled song (3) Speed of trilled song (3) Tail length (1) Total: 13	Presence / absence of rufous crown (3) Extent and shade of grey on cheek (2) Presence/absence of slow-whistling song (6) Tail length (1) Wing length (1) Total: 13	Black in moustachial concolor with head versus moustachial stripe (3) Presence / absence black on forehead (2) Grey vs. black mantle (2) Presence / absence of grey cheeks (ns [2]) Absence / presence of yellow lores (ns [1]) Presence / absence of trilled song (6) Presence / absence of cascading call (ns [6]) Wing length (1) Tail length (2) Total 16
Nominate Moustached Brush-Finch <i>A. albofrenatus</i>		Presence / absence of dark moustachial stripe (3) Extent of white on throat (2) Extent of rufous on crown (1) Presence / absence of cascading call (6) Speed and structure of trilled song (ns [>4]) Wing length (2) Tail length (1) Total: 15	Green vs. grey mantle (3) Presence / absence rufous crown (3) Presence / absence white moustachial stripe (3) Presence / absence white throat (ns[3]) Presence / absence trilled song (6) Total: 15	Green vs. black mantle (3) Presence / absence white moustachial stripe (3) Presence / absence white on throat (3) Absence / presence yellow lores (ns [1]) Presence / absence of trilled song (6) Wing length (1) Tail length (2) Total: 18
Mérida Brush-Finch <i>A. meridae</i>			Green versus grey mantle (3) Presence / absence of rufous on crown (3) Presence / absence white moustachial stripe (3) Presence/absence of trilled song (6) Absence / presence of cascading call (ns [6]) Total: 15	Green vs. black mantle (3) Presence / absence white moustachial stripe (3) Presence / absence white on throat (3) Absence / presence yellow lores (ns [1]) Presence / absence of trilled song (6) Absence / presence of slow-whistle song (ns [6]) Wing length (2) Tail length (2) Total: 19
Santa Marta Brush-Finch <i>A. melanocephalus</i>				Grey vs. black mantle (3) Absence / presence of rufous on crown (3) Presence / absence of grey on cheek (3) Absence / presence yellow lores (ns [1]) Presence / absence cascading call (6) Tail length (1) Total: 16

Table 1. (above, overleaf): scores for *Atlapetes nigrifrons* under the Tobias *et al.* (2010) system. The species first described is that in the left hand column (such that ‘grey vs. green mantle’ in the first cell refers to *nigrifrons* vs. *albofrenatus*). Biometric characters are based on Donegan & Huertas (2006). Where vocal repertoires are different such that a kind of song is not given by one taxon but not by a compared taxon, then this is scored 6, based conservatively on a score of 3 for temporal and 3 for spectral characters for non-homologous vocalizations with similar function. Because each taxon-pair is compared only once, various cells are left blank.

National Park in Colombia and create a bi-national park. However, government ratification of the new National Park has been stalled. Declaration of the park remains a high priority according to current government officials. It is vital that ProAves’ new Chamicero de Perijá Bird Reserve is expanded through land acquisition to protect one of the last areas of mature subtropical forest to páramo on the western slope of the range and also help form the core or a buffer for what may ultimately become a new National Park. Research should also focus on gathering information on the population size, trends and threats of *A. nigrifrons* which could lead to a further reclassification.

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Appendix: list of sound recordings inspected

A. *albofrenatus*: COLOMBIA Parque Natural Chicaque, Cundinamarca (04°37'N, 74°19'W, 2,100-2,500 m) (XC24076, 37128, 37564-5: O. Cortes; XC23508-10: T. Donegan). Laguna de Pedro Palo, Cundinamarca (04°39'N, 74°23'W, 2,000 m) (XC12483: O. Laverde; XC84263-6 (= Boesman 2012, tracks 3066-2 and 7): A. Spencer). Reserva Iguaque (SFF), Villa de Leyva, Boyacá (3,000m) (XC45463, 56049-50: B. López-Lanús; Álvarez *et al.* 2007, track 22a: José Agustín López). El Talisman, San Vicente, Serranía de los Yariguies, Santander (06°50'N, 73°21'W, 2,000 m) (XC44640: T. Donegan). RNA Hormiguero de

Torcoroma, Ocaña, Norte de Santander (08°12'N, 08°12'W, 1,750 m) (XC16561-2, 16689 (= Boesman 2012, track 3066-3): F. Lambert; XC102521: F. Schmitt; XC22343-6: A. Spencer; XC14033-4 (=Boesman 2012, track 3066-5): B. Davis; XC10741 (=Boesman 2012, track 3066-6): N. Athanas). Ocaña, Agua de la Virgen, Cerro de la Virgen, Norte de Santander (08°13'N, 73°24'W, 1,600 m) (XC12430, 12609, 12617-8, 12443, 12670 and Álvarez *et al.* 2007, tracks 22b-d: O. Laverde; XC20515, 62650, 203108 (= whole track of XC44734): T. Donegan).

A. *meridae*: VENEZUELA: Pico Humboldt Trail, near Tabay, Mérida (09°30'N, 71°00'W) (ML40443: P. Coopmans). Hotal Páramo La Culata (08°44'N, 71°05'W, 2,746 m) (ML178436: J. W. McGowan). La Azulita, Mérida (08°43'N, 71°27'W, 1800m) (ML63597-9: P. Schwartz; ML55732-3: D. Fisher, Boesman 2012, track 3066-4= XC202428: H. Matheve; XC197555: J. Klaiber). Bosque Experimental de la Universidad de Los Andes, Mérida (08°39'N, 71°24'W, 2,200 m) (XC6880 = Boesman 2007: N. Athanas). West of Mérida (08°36'N, 71°09'W, 1,905 m) (ML102532: L. R. Macaulay). El Morro road, Merida, Venezuela, 08°30'N, 71°05'W) (Boesman 2012, track 3066-1 = Boesman 2007: P. Boesman).

A. *nigrifrons*: COLOMBIA: Reserva Natural de Aves 'Chamicero de Perijá', Manaure, depto. Cesar (10°22'N 72°57'W, 1,700-2,400 m) (XC203102: P. Salaman; XC203103-5: A. Quevedo).

A. *latinuchus yariguierum*: COLOMBIA: Filo Pamplona, Serranía de los Yariguies, Galan, Santander, (06°38'N, 73°24', 3,200 m) (XC26832-33, 64558: T. Donegan). Soatá, Alto Onzaga, Santander (06°34'N, 72°44'W, 2,500 m) (XC12679-81: O. Laverde). Lepipuerto, Serranía de los Yariguies (06°27'N, 73°27'W, 2,900 m) (XC6484, 24013-14, 24016, 24034, 24037: T. Donegan). Rogitama (Reserva Principe de Arcabuco) (05°46'N, 73°26', 2,300 m) (XC91762, 194451: O. Cortés; Alvarez *et al.* 2007, track 30d: M. Álvarez-R.). Sutamarchán, Serranía de Merchán, vereda El Eermitaño, Boyacá (Alvarez *et al.* 2007, track 30e: M. Álvarez-R.).

A. *latinuchus eleaoprorus*: COLOMBIA: Páramo Belmira (06°37'N, 75°38', 3,000 m) (XC76988: P. Florez). La Lana, San Pedro de los Milagros, Antioquia (06°26'N, 75°35'W, 2, 650 m, 2,740 m, 2,700 m) (XC39532-33, 39565, 39569-74, 39557-58: T. Donegan). Medellín, vereda El Plan (Alvarez *et al.* 2007, track 30b: A. M. Cuervo). Envigado, vereda Alto de El Escobero, Antioquia (Alvarez *et al.* 2007, track 30a: A. M. Cuervo). Alto de Boquerón (arriba), Vereda

Boquerón, San Cristóbal, Medellín, Antioquia (2,300 m) (XC56075-7: B. López-Lanús).

A. *latinuchus caucae*: Entre La Romelia y El Planchon (PNN Munchique), Charguayaco, Vereda La Romelia, Mun. El Tambo, Cauca (2,300 m) (XC56417-8: B. López-Lanús). Popayán, 12 km sobre la carretera a Totoro (Alvarez *et al.* 2007, track 30c: D. N. Ewert).

A. *latinuchus spodionotus*: COLOMBIA San Juan de Pasto, Corregimiento de Daza, Nariño (01°16'N, 77°15', 2,800 m) (XC12705, Alvarez *et al.* 2007, track 30g: O. Laverde; Alvarez *et al.* 2007, track 30f: D. P. Moncayo). ECUADOR Parque Nacional Cayambe Coca - Laguna San Marcos (00°06'N, 77°57'W, 3,400 m) (XC109782: L. Ordóñez-Delgado). Bellavista, Pichincha (00°01'S, 78°41'W, 2,300 m) (XC128181: J. Fischer). Tandayapa Valley, Pichincha (00°01'S, 78°41'W, 2,300 m) (XC6667: N. Athanas). Old Chiriboga Road, Pichincha (00°15'S, 78°45'W, 2,450 m) (XC9286: A. Chartier). Cotopaxi NP, Pichincha (00°39'S, 78°28'W, 3,800 m) (XC9285: A. Chartier).

A. *latinuchus comptus*: ECUADOR Lagunas de Manú (Saraguro - Loja) (03°34'S, 79°25'W, 3,400 m) (XC154560: L. Ordóñez-Delgado). Quebrada Las Vegas, E. Alamor, Loja (1,500 m) (XC16436: C. Vogt). Bosque Protegido Huashapamba, Loja (03°39'S, 79°16'W, 2,800 m) (XC61410-11: A. Spencer). Acanama, Loja (03°40'S, 79°14'W) (XC30915: A. Spencer). Parque Universitario, Universidad Nacional de Loja (04°02'S, 79°11'W, 2,200 m) (XC99949: L. Ordóñez-Delgado). PERU Bosque de Cuyas, Ayabaca, Piura (04°38'S, 4°38', 2,800 m) (XC745: W. Vellinga) (latter, perhaps of subsp. *chugurensis* whose limits were not studied here).

A. *latinuchus latinuchus*: (some Peruvian recordings may be of subspecies *baroni*, whose limits were not studied here) ECUADOR Bosque Protector Cooperativa Jima Ltda. (Gualaquiza - Morona Santiago) (03°17'S, 78°53'W, 3,000 m) (XC131656-58, XC132409, XC133355: L. Ordóñez-Delgado). Reserva Tapichalaca, Valladolid, Zamora-Chinchipe (04°29'S, 79°07'W, 2,400 m) (XC20263: C. Vogt; XC30916: A. Spencer; XC38786: F. Lambert). Quebrada Honda (arriba), Zamora-Chinchipe (XC50423: B. López-Lanús). PERU Abra Patricia, San Martín (05°40'-42'S, 77°45'-48', 2,000-2,300 m) (XC14443: R. Ahlman; XC35961: F. Lambert; XC102642: F. Schmitt; XC180397, 180236: M. Nelson; XC194668-9: D. Caiafa). Upa, Amazonas (06°00'S, 77°50'W) (ML147701, 147704: F. Angulo). Bosque Paja Blanca, Chotas, Cajamarca (06°23'S, 79°07'W, 2,700 m) (XC37695: B. Planqué; XC55223, 152331, 152325: W. Vellinga). Bosque protector Pagaibamba, Chotas, Cajamarca (06°26'S, 79°4', 3,000 m) (XC23665-6: W. Vellinga).

A. *melanocephalus*: COLOMBIA RNA El Dorado or San Lorenzo, Sierra de Santa Marta, Magdalena (11°06'N, 74°04'W, 1,800-2,600 m) (XC10156-7: C. Hesse; XC10751: N. Athanas; XC15628: D. Bradley; XC37111: M. Ritschard; XC43461, 43464-5, 43474, 43521-3: T. Donegan; XC45461, 56805: B. López-Lanús; XC152280: O. Cortés; XC165426-44: N. Krabbe; XC18088: H. van Oosten; ML68035, 68038, 68060, 68073, 68088: P. Coopmans; ML167138, 167144, 167172, 167176, 167246, 167269, 167287: M. Sarver).