



Geographic variation and phylogenetic relationships of *Myiopagis olallai* (Aves: Passeriformes; Tyrannidae), with the description of two new taxa from the Northern Andes

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Abstract

Geographic variation in vocalizations, morphology and plumage patterns in New World flycatchers is little understood, particularly in rare species with disjunct distributions. We discovered a distinct new flycatcher of the genus *Myiopagis* from cloud forests of the northern Central Andes in Antioquia, Colombia. Comparisons of vocalizations and external morphology, and molecular phylogenetic analyses, demonstrate that the “Antioquia *Myiopagis*” is a unique lineage of the *M. caniceps-olallai* group. We show that three specimens collected in 1940–1951 from cloud forests of Serranía de Perijá in Venezuela, and traditionally assigned to *M. caniceps*, represent another distinct taxon that is closer to the “Antioquia *Myiopagis*” and *M. olallai*. Both new taxa, from Antioquia and Perijá, are described as subspecies of *M. olallai*. We present a phylogenetic hypothesis for the *M. caniceps-olallai* group, in which *M. olallai* and the “Antioquia *Myiopagis*” are phylogenetically nested within the polytypic *M. caniceps*, which consists of at least four distinct lineages, indicating that species diversity in this group could be underestimated.

Key words: Andes, Colombia, cloud forest, Foothill Elaenia, Serranía de Perijá, species tree, Venezuela, vocalizations

Introduction

The suboscine passerines of the New World have long presented challenges for taxonomy and systematics because traditional morphological assessments are often misleading with regard to evolutionary relationships. Morphology, plumage patterns and coloration can vary subtly across species or be highly homoplasious in this diverse clade (e.g., Birdsley 2002; Ohlson *et al.* 2009; Hosner & Moyle 2012). The innate nature of vocalizations in nearly all suboscines (Kroodsma 1984; Kroodsma & Konishi 1991; Saranathan *et al.* 2007, Touchton *et al.* 2014) has been instrumental in redefining species limits (Isler *et al.* 1998; Renssen 2005), especially when combined with molecular phylogenetic data (Isler *et al.* 2012). The concordance between vocal and phylogenetic variation to elucidate species boundaries has demonstrated that diversity of Neotropical suboscines has been greatly underestimated in the past. Although the most striking example of this is found in the family Rhinocryptidae, in which the number of independent lineages and recognized biological species has increased fourfold in the past two decades (Krabbe & Schulenberg 2003; Cuervo *et al.* 2005; Mata *et al.* 2009; Krabbe & Cadena 2010; Maurício *et al.* 2014), numerous hitherto undetected species have been found in other suboscine lineages as well, e.g., Thamnophilidae (Chaves *et al.* 2010; Whitney *et al.* 2013), Grallariidae (Carantón-Ayala & Certuche-Cubillos 2010; Carneiro *et al.* 2012), Tityridae (Nyári 2007) and Tyrannidae (Rheindt *et al.* 2013; Zimmer *et al.* 2013). Often cryptic species are first detected by their vocalizations and then confirmed through more detailed examination of specimens and subsequent phylogenetic analyses. These discoveries were largely due to increasing

knowledge of vocalizations and archiving of sound recordings (Parker 1991; Schulenberg & Parker 1997; Zimmer & Whittaker 2000), and to the continued collecting of modern specimens associated with behavioral and vocal data (e.g. Álvarez-Alonso & Whitney 2001; Whitney *et al.* 2010; Zimmer *et al.* 2013). A notable case in point in the Tyrannidae is the discovery of the rare species *Myiopagis olallai* (Foothill Elaenia) in the Andean foothills of eastern Ecuador by Paul Coopmans in 1992 on the basis of *in situ* recognition of its distinct vocalizations (Coopmans & Krabbe 2000).

The genus *Myiopagis* Salvin and Godman (1888) as currently defined (Zimmer 1941; Fitzpatrick 2004), comprises seven species of fairly small tyrant-flycatchers that in general aspect superficially resemble members of the genus *Elaenia* Sundevall (Zimmer 1941; Traylor 1977), a group of birds notoriously difficult to identify. Members of *Myiopagis* differ from those of *Elaenia* in their slightly smaller size, the shape and proportions of bill, wings, and feet, their often yellow instead of white crown patch (cf. Ridgway 1907), and their tarsal scutellation (cf. Zimmer 1941; Coopmans & Krabbe 2000). An additional difference is the existence in *Myiopagis* but not *Elaenia* of a concealed horny spur on the leading edge of the wing just proximal to the tip of the alula, a character also present in *Zimmerius* Traylor and some *Phyllomyias* Cabanis & Heine (D. Agro cited in Coopmans & Krabbe 2000). As in *Elaenia*, several *Myiopagis* species are confusingly similar to each other in plumage but differ in vocalizations (Coopmans & Krabbe 2000), such that species diversity and distributional ranges are probably underestimated.

In this study, we compare vocal data and museum specimens to show that the distribution of *M. olallai* in the Andes has been underappreciated, and describe two taxa that are restricted to the northern Central Cordillera of Colombia and the Serranía de Perijá in Venezuela. Molecular phylogenetic analyses were conducted to evaluate predictions of phylogenetic affinities derived from vocal and plumage patterns, and to examine the evolutionary divergence of the Andean *M. olallai* populations in relation to the lowland and polytypic *M. caniceps* complex.

Methods

Specimens and vocalizations. Sightings and sound recordings of an unidentified *Myiopagis* flycatcher with light-gray underparts and green back have been made since 24 May 1999 by AMC and co-workers during an ongoing study of the avifauna of the Andean region of northwestern Colombia (e.g., Cuervo *et al.* 2005; Cuervo *et al.* 2008b). A male specimen was collected on 5 January 2005 at 1825 m at Bosque Guayabito in Amalfi, Antioquia (Fig. 1). This specimen exhibits distinct plumage differences from other *Myiopagis* species, albeit somewhat resembling the female plumage of larger-sized *M. c. caniceps* of southern Amazonia and southeastern South America. Based on examination of photographs of this new specimen, P. Coopmans (pers. comm., 28 May 2005) suggested it must represent an undescribed species. However, the publication of sound recordings of the yellowish *M. olallai* (Coopmans & Krabbe 2000) from the Ecuadorian Andes (Lysinger *et al.* 2005; Krabbe & Nilsson 2007) later led us to recognize the vocal similarity of the “Antioquia *Myiopagis*” to the recently described *M. olallai*. Indeed, P. Coopmans commented that our song recordings “matched undoubtedly” those of *M. olallai* (pers. comm. 29 July 2006).

Using playback of *M. olallai* recordings from Ecuador (Krabbe & Nilsson 2007), we attracted several individuals of the “Antioquia *Myiopagis*” and collected a second male specimen at a different locality at 1,500 m in Bodega Vieja, Amalfi. We investigated in ornithological collections the existence of *Myiopagis* specimens that resembled the newly discovered grayish population and that could have been overlooked or misidentified. We found three specimens collected between 1940 to 1951 from the eastern slope of Serranía de Perijá, Venezuela that resemble the two male “Antioquia *Myiopagis*” specimens in several respects. The Perijá specimens had been interpreted traditionally (i.e., Phelps 1943; Ginés *et al.* 1953; Traylor 1979) as extralimital records of *M. caniceps cinerea* (Pelzeln 1868), a taxon from northern and western Amazonia (Hilty 2003; Fitzpatrick 2004). We compared these intriguing specimens from Colombia and Venezuela directly (or by means of recent photographs) with specimens of *M. olallai* and *M. caniceps*, including the types of most described forms (Appendix 1).

We expanded on a previous general description of vocal variation in *Myiopagis* flycatchers (Coopmans & Krabbe 2000), and examined 16 audio recordings of the pale-gray population from Antioquia and 20 of *M. olallai* from Ecuador and Peru (Appendix 2). Vocalizations were obtained from our fieldwork (archived at the IAVH-BSA), published commercial compilations (Lysinger *et al.* 2005; Krabbe & Nilsson 2007), and the online sound

archive xeno-canto (XC, <http://www.xeno-canto.org>). However, in spite of recent field work in Serranía de Perijá (Lentino *et al.* 2004; López-O. *et al.* 2014) no sound recordings were available for that population. We reviewed the metadata of recordings to identify songs and calls, and the number of individuals vocalizing. The sample unit for statistical analysis was the individual bird; hence we calculated the average value of each vocal trait across song bouts per individual. After excluding low quality recordings, we compared statistically the post dawn songs of eight individuals (11 bouts, all natural songs) of the Antioquia population with those of nine of *M. olallai* (19 bouts, including natural and response songs to playback). Dawn songs, calls and rattles have not been sufficiently documented in these birds to be useful for comparative analyses. Using the program Syrinx (1024 points, Blackman FFT window), audio spectrograms and oscillograms were prepared for every song and call delivered by each individual. We quantified song duration, number of notes, and frequency (minimum, maximum, and bandwidth). The low sample size of high-quality recordings prevented measuring additional spectral variables or comparisons of alternative vocalizations.



FIGURE 1. Photograph of the “Antioquia *Myiopagis*” exhibiting some of the characteristics, including light gray underparts, mossy green back, dark gray head, immaculate white crown patch, and reddish-brown eyes, that distinguish it from other taxa. Collected in an Andean cloud forest (1825 m) at Bosque Guayabito, Amalfi, Department of Antioquia, Colombia (ICN 35903).

Laboratory protocols and phylogenetic analysis. A previous molecular phylogenetic analysis of *Myiopagis* (Rheindt *et al.* 2009) suggested that the genus is monophyletic, although samples of the Jamaican endemic *M. cotta* were not included. Rheindt *et al.* (2009) included mitochondrial sequences from blood samples of the two type specimens of *M. olallai* from Zamora-Chinchipec, Ecuador (Coopmans & Krabbe 2000; Rheindt *et al.* 2009). To ascertain the phylogenetic placement of the newly discovered pale-gray *Myiopagis* population from Antioquia with respect to *M. olallai* and *M. caniceps*, we sequenced the mitochondrial gene NADH dehydrogenase subunit 2 (ND2) and the autosomal nuclear intron 5 of the b-fibrinogen gene (FGB-5) for the two available Antioquia specimens as well as for six individuals of *M. caniceps* from disjunct areas, including the subspecies *parambae*, *cinerea*, *caniceps*, and individuals of a possibly undescribed form (aff. *caniceps*). We selected molecular markers and outgroup taxa, guided by the available data from previous phylogenetic studies of tyrant-flycatchers (Rheindt *et al.* 2008; Rheindt *et al.* 2009). One member of each *Myiopagis* species (the nominate subspecies, when available) and three more distantly related tyrannid lineages were selected for the outgroup (Table 1). Tissue samples were unavailable for the montane population of *Myiopagis* from Perijá and the Panamanian subspecies *M. caniceps absita*.

DNA was extracted from ~20 mg of pectoral muscle tissue using a DNeasy tissue kit (Qiagen, Valencia, CA), following the manufacturer’s protocol. For ND2 (1041 bp), we used the primers L5215 (Hackett 1996) and H6313 (Johnson & Sorenson 1998) for amplification and sequencing, and internal sequencing primers L5758 and H5766

for double sequencing coverage (Sorenson *et al.* 1999; Brumfield *et al.* 2007). For FGB-5 (580-548 bp), we used the primers Fib5 and Fib6 (Kimball *et al.* 2009). Each 25 μ l PCR contained 2.5 ml of template (~50 ng of genomic DNA), 2.5 ml of 10X buffer with MgCl₂ (15 mM), 0.5 μ l of 10 mM dNTPs (2.5 mM each), 0.75-1.0 ml of each primer (10 mM), 0.1 ml (5 units/ml) of *Taq* DNA polymerase (New England Biolabs, Ipswich, MA), and 17.4-17.9 ml of sterile dH₂O. The thermocycling conditions were as follows: an initial denaturation for 2 min at 94°C, followed by 35 cycles of denaturation for 30 sec at 94°C, 30 sec of annealing (50°C for ND2 and 54°C for FGB-5), extension 1 min at 72°C, and a final extension step for 7 min at 72°C. Amplicons were visualized by electrophoresis in 1% agarose gel and purified using 20% polyethylene glycol (PEG) precipitation. Purified amplicons were cycle-sequenced on 7 ml reactions using 0.3 ml of Big Dye Terminator cycle-sequencing kit 3.1 (Applied Biosystems, Foster City, CA), purified with Sephadex columns (G-50 fine), and sequenced on an ABI 3100 Genetic Analyzer. Raw sequence data were inspected, edited, and aligned using Sequencher 4.7 (GeneCodes Corp., Ann Arbor, MI). For FGB-5, heterozygous sites were coded using the IUPAC ambiguity codes and the alignment was assembled using Muscle (Edgar 2004) coupled with Geneious (Drummond *et al.* 2011).

TABLE 1. *Myiopagis* tissue samples used this in the phylogenetic analysis. Asterisks represent accession numbers of data downloaded from GenBank (Rheindt *et al.* 2008; Rheindt *et al.* 2009), all others where generated in this study (ND2 left, FGB-5 right). Elevation above sea level (in meters) is given in parenthesis.

Taxon	Sample	GenBank Accession	Locality
<i>Serpophaga subcristata</i>		*EF501914, EF501846	Argentina
<i>Elaenia frantzii</i>		*EU311059, EU311120	El Salvador
<i>Tyrannulus elatus</i>		*EF501922, EF501833	Bolivia: Beni
<i>M. subplacens</i>	LSUMZ-B5214	KM369999, KM369987	Peru: Lambayeque, Las Pampas (90)
<i>M. gaimardii</i>	LSUMZ-B28653	KM370000, KM369988	Panama: Panama, 7 km W Paraiso (360)
<i>M. flavivertex</i>	LSUMZ-B42865	KM370001, KM369989	Peru: Loreto, 54 km NNW mouth Río Morona (175)
<i>M. viridicata</i>	LSUMZ-B26883	KM370002, KM369990	Panama: Panama, 5 km NW Paraiso (ca. 75)
<i>M. caniceps caniceps</i>		*EU310971, EU310957	Paraguay: San Pedro, San Rafael N.P. (ca. 150)
<i>M. caniceps caniceps</i>	LSUMZ-B6656	KM370003, KM369991	Bolivia: Santa Cruz, 3 km W Santiago by rd (100)
<i>M. caniceps</i> aff. <i>caniceps</i>	LSUMZ-B1048	KM370006, KM369994	Bolivia: La Paz, 20 km by river N Pto. Linares (ca. 600)
<i>M. caniceps</i> aff. <i>caniceps</i>	LSUMZ-B58379	KM370004, KM369992	Peru: Puno, 25 km NE San Juan de Oro (ca. 900)
<i>M. caniceps</i> aff. <i>caniceps</i>	LSUMZ-B58393	KM370005, KM369993	Peru: Puno, 25 km NE San Juan de Oro (ca. 900)
<i>M. caniceps cinerea</i>	LSUMZ-B42867	KM370007, KM369995	Peru: Loreto, 54 km NNW mouth Río Morona (ca. 175)
<i>M. caniceps parambae</i>	LSUMZ-B29982	KM370008, KM369996	Ecuador: Esmeraldas, 30 km SE San Lorenzo (ca. 85)
<i>M. olallai</i>		*EU310975, n.a.	Ecuador: Zamora-Chinchi (1000)
<i>M. olallai</i>		*EU310976, n.a.	Ecuador: Zamora-Chinchi (1000)
" <i>Antioquia Myiopagis</i> "	ICN 38437 (holotype)	KM370009, KM369997	Colombia: Antioquia, Amalfi, Bodega Vieja (1500)
" <i>Antioquia Myiopagis</i> "	ICN 35903 (paratype)	KM370010, KM369998	Colombia: Antioquia, Amalfi, Bosque Guayabito (1825)

Bayesian inference (BI) in MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003) and a maximum likelihood analysis (ML) in RAxML 7.2.6 (Stamatakis 2006) were used to estimate each gene tree via the CIPRES Science Gateway

3.1 portal (Miller *et al.* 2010). Four Markov Chain Monte Carlo (MCMC) chains were run in MrBayes for 10 million generations, sampling parameters and trees every 1,000 steps, of which the first 25% were discarded as burn-in. The selected nucleotide substitution models were GTR+I+ Γ for ND2 and HKY+I for FGB-5 based on the Akaike information criterion using MrModelTest 2.3 (Nylander 2004) in conjunction with PAUP* 4.0b10 (Swofford 2002). The ML analysis implemented the GTR+G model of nucleotide substitution and 25 rate categories for Γ to account for invariant sites as recommended by the RAxML author (Stamatakis 2006), and used the automatic rapid bootstrapping option to assess nodal support based on 1000 bootstrap replicates. Obtained trees were rooted between outgroup and ingroup taxa.

We conducted a coalescent-based species-tree analysis that accounts for deep coalescence of gene trees along the species tree and the discordance among gene trees. We estimated the species tree for the differentiated lineages of *Myiopagis caniceps* and *M. olallai* by jointly estimating the ND2 and FGB-5 gene trees under a Bayesian framework as implemented in the program BEST 2.3 (Liu 2008). Two independent analyses of two MCMC chains were run for 100 million generations, with a heating temperature of 0.15, sampling every 10,000 steps, and discarding the 50% as burn-in. The BEST-exclusive prior for the scaled population size (theta) was an inverse gamma distribution with $a = 3$ and $b=0.1$, and the prior for the mutation rate, a uniform distribution with bounded values 0.1 and 3. Convergence among MCMC chains and runs well after the burn-in cutoff were confirmed for the BI and BEST analyses using Tracer 1.5 (Rambaut & Drummond 2007) and plots of the split frequencies using AWTY (Nylander *et al.* 2008).

Results

Vocalizations. The song of the grayish *Myiopagis* from Antioquia is a rapid trill that consists of two parts. The song begins with a short segment of distinct whistles (i.e., 2–4 introductory notes) and continues with a trill of chevron-shaped notes that rises gradually in pitch and then levels off with a longer monosyllabic repeat at a constant pace. The ascending song of the “Antioquia *Myiopagis*” is distinctly different in several spectral and temporal traits from the descending songs of subspecies of the lowland *M. caniceps* (Fig. 2); thus, we refrained from making detailed comparisons with that species. In contrast, songs from the Antioquia bird qualitatively resemble songs of *M. olallai* of Ecuador and Peru in spectral structure and note shape, but differ significantly in song pace (t-test = 4.9, $df = 11.3$, $p < 0.001$), song duration (t-test = 2.8, $df = 14.9$, $p = 0.015$), number of trill notes (generalized linear model, quasipoisson $F = 12.0$, $p < 0.005$), and in the frequency of the constant trill segment (minimum frequency t-test = 3.4, $df = 9.9$, $p < 0.01$; maximum frequency t-test = 2.1, $df = 11.3$, $p = 0.055$).

“Antioquia *Myiopagis*” songs are faster than those of *M. olallai*, produced at 20.8 ± 0.8 notes per second vs. 17.4 ± 1.9 notes per second. Although “Antioquia *Myiopagis*” songs tend to be longer (2.3 ± 0.6 vs. 1.5 ± 0.6 seconds), there is considerable overlap in song length. On average, the song phrases of “Antioquia *Myiopagis*” (excluding introductory syllables) consist of ca. 34% more notes than *M. olallai* songs, (47.1 ± 14.2 vs. 29.5 ± 11.7 notes), even though the number of notes in the song was variable in both populations. Finally, the trill segment (i.e., monosyllabic repeat at the end of the song at a constant frequency) of the “Antioquia *Myiopagis*” tended to be produced at a slightly higher frequency, but the frequency bandwidth did not differ significantly (Fig. 3).

Introductory notes in the “Antioquia *Myiopagis*” were either simple down strokes (frequency range: 6.3 to 2.9 kHz) or modulated down-up-down strokes of narrow (5.6 to 3.7 kHz) or wide (7.3 to 3.3 kHz) frequency bandwidth, and closely resembled those of *M. olallai* in quality and pattern. Different call note types have been recorded in Antioquia and are higher pitched than those of *M. olallai* (e.g. 7.1–3.4 vs. 5.7–3.2 kHz), but sample size is still too limited for a compelling comparison (Fig. 4).

Some vocalizations documented for *M. olallai* have not yet been recorded in the newly discovered population in Antioquia, including: (1) a descending short trill of 6–10 notes (e.g., cut 2 in Lysinger *et al.* 2005, XC61013, XC70742, XC70745, XC105085) that is given alone or following down stroke calls or preceding a song bout, (2) a series of high pitched notes of variable frequency added as a terminal trill to the typical song (e.g., cut 6 in Krabbe & Nilsson 2007, XC62220), and (3) a secondary song that consists of a trill of alternating chevron-shaped notes that differ in pitch and frequency range (e.g., XC70742, XC70745, XC97993 from Ecuador) or descending and ascending in pitch as in some playback songs (e.g., cuts 7 and 8 in Krabbe & Nilsson 2007). Only one recording of the “Antioquia *Myiopagis*” resembles the latter type (IAvH-BSA 19218). Some of these song types (e.g., XC3509, IAvH-BSA 19552) could correspond to female songs or intrapair vocal combinations. Dawn songs are unknown.

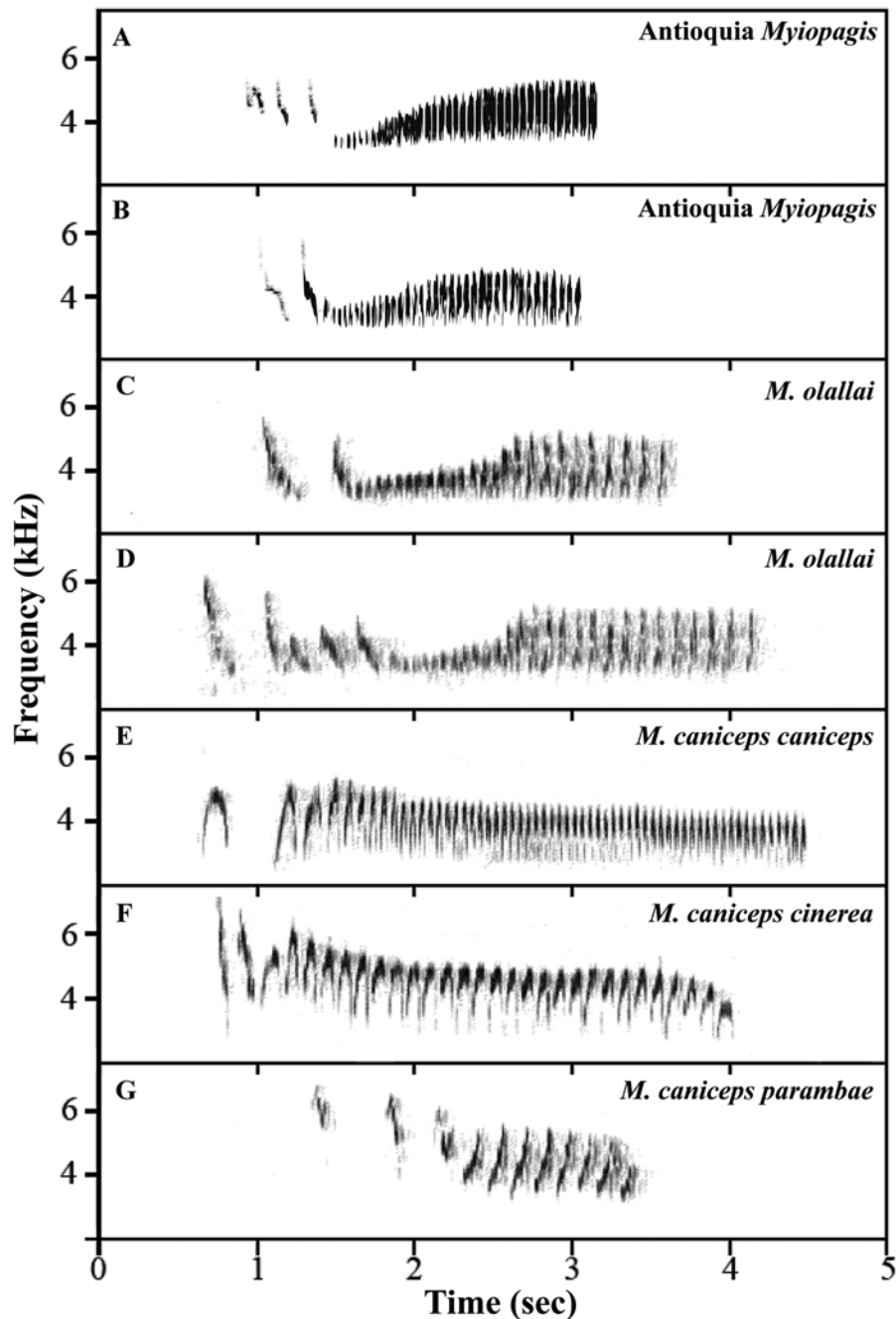


FIGURE 2. Spectrograms of songs of selected *Myiopagis* flycatchers. (A) Andean grayish form from Bosque Guayabito, Amalfi, Antioquia, Colombia (IAvH-BSA 19580 by AMC, 24 January 2002); (B) Andean grayish form from Bosque Las Ánimas, Amalfi, Antioquia, Colombia (IAvH-BSA 19187 by AMC, 8 February 2002); (C and D) *M. olallai* from the type locality, Zamora-Chinchipec, Ecuador (ML 60232 by P. Coopmans, 20 June 1992); (E) *M. caniceps caniceps* from Río Grande do Sul, Brazil (ML 19532 by W. Belton, November 1975); (F) *M. caniceps cinerea* from Napo, Ecuador (by N. Krabbe, October 1994); (G) *M. caniceps parambae* from Pichincha, Ecuador (by P. Coopmans, February 1995). Panels C-G based on figure 1 in Coopmans & Krabbe (2000); reprinted with the written permission of the Wilson Ornithological Society, 3 February 2012.

Phylogenetics. We analyzed 18 sequences of ND2 (1041 bp) and 16 of FGB-5 (548 bp). Sequence variation was greater in the mitochondrial gene ND2 than in the nuclear intron FGB-5, as expected. The proportion of variable/parsimony-informative sites was 0.417/0.289 of 1041 sites for ND2, 0.144/0.066 of 548 sites of FGB-5. The quality of the raw traces and sequence characteristics of the mtDNA gene confirm that we obtained our target region and not nuclear pseudogenes (Arctander 1995; Sorenson & Quinn 1998).

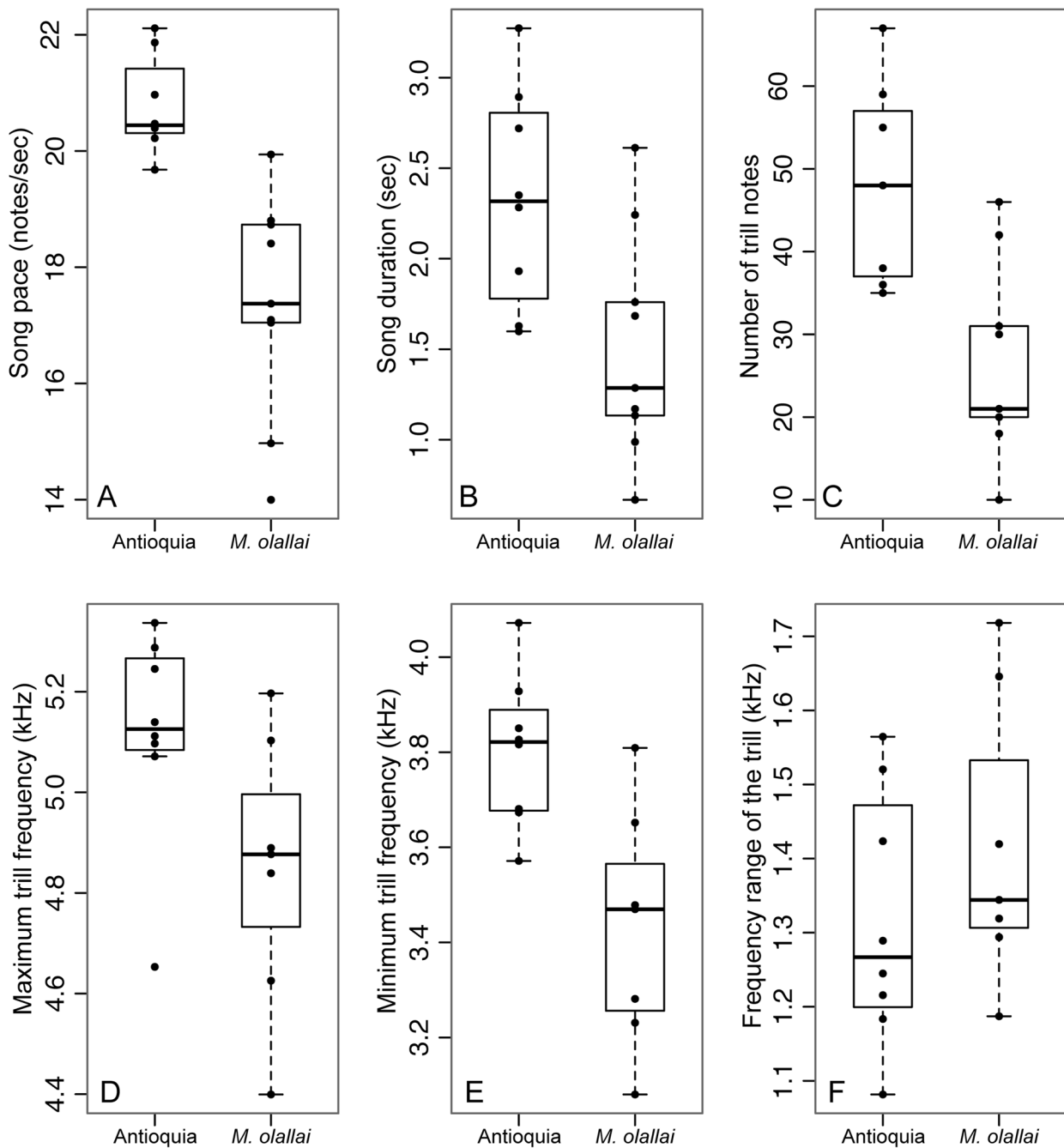


FIGURE 3. Box plots comparing the “Antioquia *Myiopagis*” and *M. olallai* in six song attributes. (A) song pace; (B) song duration; (C) number of notes in the trill part of the song; (D) maximum and (E) minimum frequency of the trill; (F) frequency range of the trill (non significant). Data points represent the average values per individual bird.

The “Antioquia *Myiopagis*”, *M. olallai*, and *M. caniceps* formed a strongly supported clade within the genus in the ND2 tree (Fig. 5A). The “Antioquia *Myiopagis*” samples were sister to *M. olallai* samples of Ecuador, and in turn were phylogenetically nested within *M. caniceps*. Uncorrected sequence divergence of the “Antioquia *Myiopagis*” from *M. olallai* averaged 0.6%, and ranged between 4.7% and 8.2% between the “Antioquia *Myiopagis* and *M. caniceps* (Table 2). Differentiation between some lineages of *M. caniceps* exceeded that range (e.g., 9.8% between *cinerea* and aff. *caniceps*). The FGB-5 tree also exhibited differentiation of the “Antioquia *Myiopagis*” with respect to *M. caniceps* subspecies, particularly *M. c. cinerea* and *M. c. parambae* (Fig. 5B). A 3-bp indel was synapomorphic for the *caniceps-olallai* clade. The BEST species tree also showed that the “Antioquia *Myiopagis*” makes *M. caniceps* paraphyletic, and indicated with strong support that this montane taxon is more

closely related to the southern populations of *M. caniceps*, including the nominate subspecies, than to the northern taxa *parambae* and *cinerea*. The BEST tree differed from the ND2 tree in the sister relationship of *M. c. cinerea* and of *M. c. parambae* to the rest of *M. caniceps* and *M. olallai* (Fig. 6).

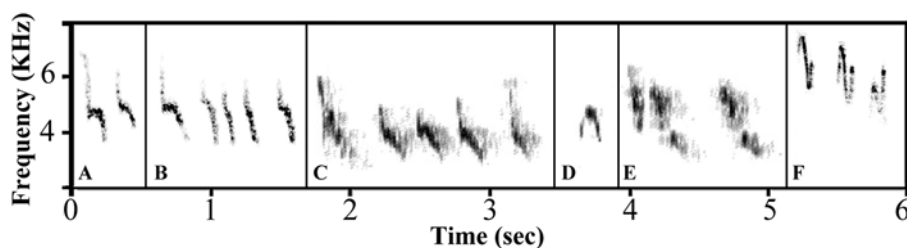


FIGURE 4. Spectrograms of call vocalizations in *Myiopagis olallai* and its closest relatives. (A) Andean grayish form from Bosque Guayabito, Amalfi, Antioquia, Colombia (IAvH-BSA 19543 by AMC, 21 January 2002); (B) Andean grayish form from Bosque Las Ánimas, Amalfi, Antioquia, Colombia (IAvH-BSA 19218 by AMC, 11 February 2002); (C) *M. olallai* from type locality, Zamora-Chinchipec, Ecuador (ML60232 by P. Coopmans, 20 June 1992); (D) *M. caniceps caniceps* from Río Grande do Sul, Brazil (ML 19532 by W. Belton, November 1975); (E) *M. caniceps cinerea* from Napo, Ecuador (by N. Krabbe, October 1994); (F) *M. caniceps parambae* from Imbabura, Ecuador (XC71233 by D. F. Lane, 14 July 1997). Panels C, D, and E based on figure 2 in Coopmans & Krabbe (2000); reprinted with the written permission of the Wilson Ornithological Society, 3 February 2012.

TABLE 2. Average sequence divergence (uncorrected *p* distance of the mitochondrial ND2 gene) between lineages of the *Myiopagis caniceps-olallai* clade. Note the strong divergence of the newly discovered Andean *Myiopagis* from Antioquia, Colombia (6) with respect to all sampled taxa in the polytypic *M. caniceps* (1–4), but the slight differentiation with *M. olallai* of the eastern Andean foothills of Ecuador (5).

	1	2	3	4	5
1. <i>M. c. caniceps</i>					
2. <i>M. c. aff. caniceps</i>	0.013				
3. <i>M. c. cinerea</i>	0.092	0.098			
4. <i>M. c. parambae</i>	0.076	0.086	0.091		
5. <i>M. olallai</i>	0.049	0.056	0.086	0.079	
6. “Antioquia <i>Myiopagis</i> ”	0.047	0.055	0.082	0.078	0.006

Plumage variation. The vocal and genetic evidence presented above indicated close affinities and slight differentiation of the “Antioquia *Myiopagis*” from *M. olallai* of Ecuador and Peru. Upon examination of series of specimens and photographs of *M. olallai* (Fig. 7) and of *M. caniceps* from throughout its range (Fig. 8; see Appendix 1), including types, and comparisons with the two male specimens from Antioquia, we concluded that this newly discovered population is a distinctive undescribed taxon. Briefly, the Antioquia *Myiopagis* is whitish gray below with a slightly darker breast (instead of yellow underparts as in *M. olallai*), is olive-green above, has pale yellow wing bars, and a dark-gray head with a white coronal patch (unlike *M. caniceps*). The three specimens from the cloud forests of Serranía de Perijá also do not correspond to any known subspecies of *M. caniceps*, as suspected by Ginés *et al.* (1953). Instead, the Perijá specimens more closely resemble the Antioquia specimens and, to a lesser extent, topotypical *M. olallai* (except in underparts coloration, see Fig. 7). Both the Antioquia and the Perijá *Myiopagis* populations represent minimally distinct subspecies (Remsen 2010) under the biological species concept (Mayr 1942). We here propose to name these taxa as two new subspecies:

Myiopagis olallai coopmansii, taxon novum

Holotype. An adult male deposited in the ornithological collection of the Instituto de Ciencias Naturales, Universidad Nacional de Colombia (ICN 38437), from Bodega Vieja, Amalfi, Department of Antioquia, Colombia (6°58’N, 75°03’W; 1500 m elevation); collected by J. E. Avendaño and prepared by A.M.C. (field number 1355) on 29 November 2010. The holotype consists of a round museum skin with its left wing prepared as a spread wing

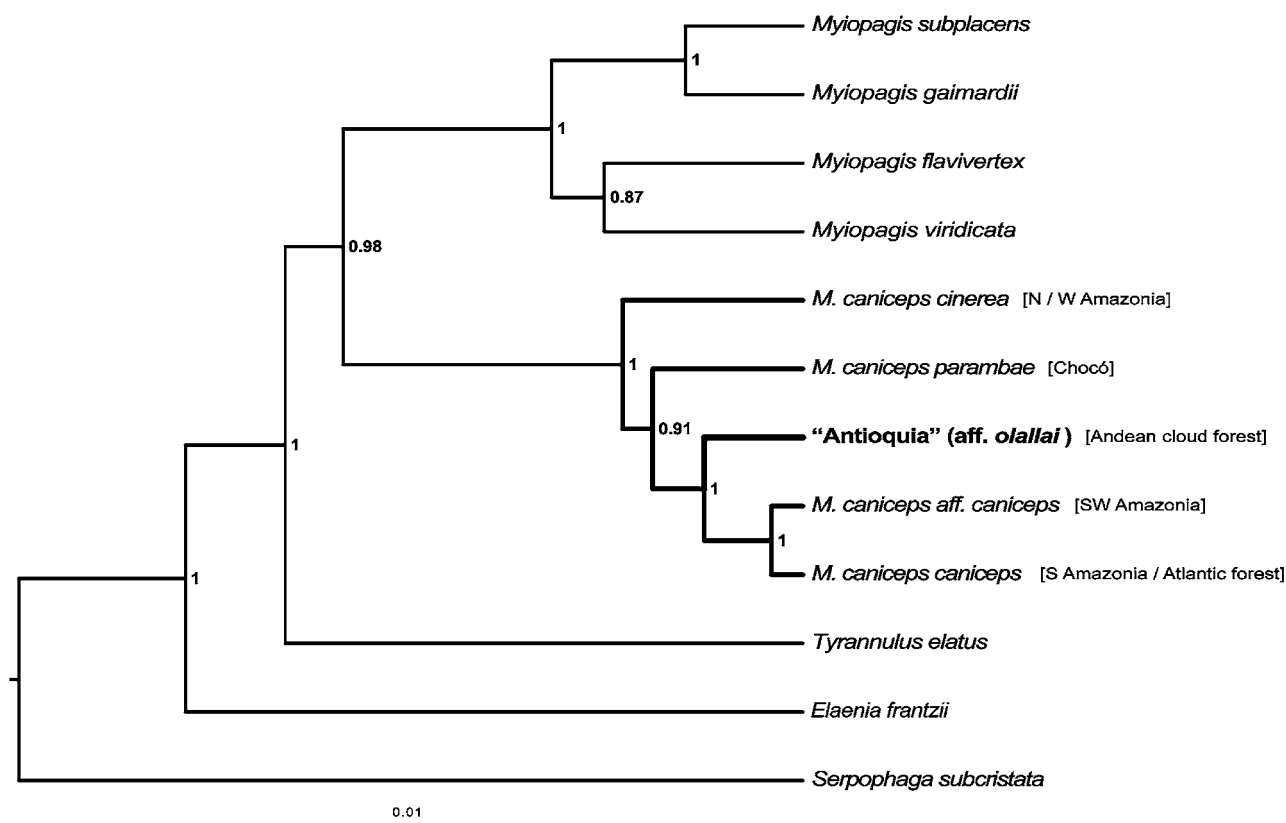


FIGURE 6. Consensus species-tree from the BEST analysis based on ND2 and FGB-5 sequences indicating Bayesian posterior probabilities of the species relationships in *Myiopagis* flycatchers. Differentiated populations from disjunct geographic regions of *M. caniceps* were treated independently. The Andean taxa in this complex are represented only by the two samples of the “Antioquia *Myiopagis*”, due to missing sequence data for one or both molecular markers for *M. olallai* and the “Perijá *Myiopagis*”. Geographic regions for each taxon in the *caniceps-olallai* group are indicated.

Diagnosis. A member of the genus *Myiopagis*, based particularly on the size and shape of the feet and the tarsal scutellation, the presence of semi-concealed coronal patch, and a horny spur next to the alula; the three wing bars align it with *M. caniceps* and *M. olallai* (cf. Ridgway 1907; Zimmer 1941; Coopmans & Krabbe 2000). Our two male specimens have completely dark olive-green backs with no trace of the gray tones that characterize adult males of all races of *M. caniceps*, and the three well-defined wing bars are pale yellow and narrow, differing from the bold white wing bars of male *M. caniceps*. Females of *M. caniceps* differ from males in the combination of gray confined to the pileum with olive-green backs, yellow wing markings, and yellow crown patches (except females of *M. c. absita* and *M. c. parambae*, which have white crown patches, Fig. 8). By contrast, *M. olallai* lacks sexual dichromatism (Coopmans & Krabbe 2000). Although we do not have a female specimen of *M. o. coopmansii*, all individuals seen in the field in pairs or as individual birds in multi-species flocks were similar to males; hence we believe that sexual dichromatism is also lacking in the new subspecies. With respect to the nominate taxon, *M. o. coopmansii* differs strongly in its whitish belly with at most a trace of pale yellow, and its plain pale olive-gray breast, as opposed to the bright yellow belly and olive-green wash across the breast with faint streaking of *M. o. olallai* (Fig. 7). Because both of our specimens are in fresh plumage, these differences cannot be due to fading. The new taxon agrees with the types of *M. o. olallai* in its reduced pale yellow wing markings and the concealed white (not yellow) crown patches, but the gray pileum is darker.

Description of holotype. Capitalized color codes follow a standard guide (Smithe 1975;1981). Forehead and crown are blackish-gray (Black Neutral Gray 82), with a dusky brown tinge on the sides (near Dusky Brown 19) and a large semi-concealed white patch on the midcrown formed by white feathers with dark gray tips (Dark Neutral Gray 83). The crown becomes paler (shading to Dark Neutral Gray 83) posteriorly, blending to olive gray on the nape (near Glaucous 79) and to dark olive green (between Basic and Auxiliary Olive Green 46–47) on the upper back. Scapulars, back, rump, and upper tail-coverts are also olive green but brighter (Bunting Green 150).

Rectrices (including rachises) are olive brown dorsally (near Van Dyke Brown 121) with lateral margins olive green (Bunting Green 150) and with a narrow tip (ca. 0.5 mm) dull buffy yellow (lighter than Cream Color 54). On the ventral surface, rectrices are light olive gray overall, shading to brownish-gray toward the tips (darker than Smoke Gray 45); their inner margins shade to olive gray (Olive-Gray 42) and rachises are yellowish white but olive towards the tip. Wings are dark brownish gray (Sepia 119), with upper wing coverts washed with olive green (Auxiliary Olive Green 47). Wings exhibit three narrow and sharply defined pale yellow bars (distal edge of outer webs lighter than Pale Sulphur Yellow 157); the two proximal bars are ca. 1.5 mm wide and the distal bar (greater coverts) 1.2 mm. Primaries have a narrow, indistinct brownish-olive margin on the outer webs (restricted to the proximal half), whereas secondaries and tertials have pale yellow tips (near Pale Sulphur Yellow 157 but paler) and well-defined edges (ca. 1 mm) on the outer webs (Fig. 9). Underwing coverts are whitish yellow, but feathers of the wrist are brownish dark gray (Vandyke Brown 221) bordered with pale yellow. From below, the flight feathers look brownish gray with inner edge yellowish. Feathers of the chin and center of the throat are dull white with indistinct pale gray borders (near Light Neutral Gray 85), giving the impression of faint, blurry streaking, shading to dull pale gray (between Glaucous 80 and Smoke Gray 44) on sides of neck and head and across breast, where forming a distinct band. The grayish breast passes fairly abruptly on the lower breast to yellowish white on the middle and posterior abdomen, and the sides are lightly smudged pale grayish. The flanks are yellowish (near Olive-Yellow 52 and lighter than Pale Sulphur Yellow 157), whereas the lower tail coverts are dull olive (paler than Auxiliary Olive Green 48). In the face, eye-ring feathers are white and cheeks mottled by feathers with pale gray centers and rachises with distal barbules dark gray (Black Neutral Gray 82). Lores show pale gray speckling and a small dark spot (near Black Neutral Gray 82) that contrast with the whitish feathers on the sides of the base of the maxilla, and black tiny soft bristles project forward around the bill. Soft parts in life as follows: iris reddish brown; maxilla black, mandible mostly black but shading to gray on base and gonys; legs and feet dark gray with black nails and yellowish soles. Wing span: 196 mm; wing length: 61.4 mm; tail at the insertion of central rectrices to the tip: 51.2 mm; tarsus: 16.2 mm; bill length from anterior edge of nares: 6.9 mm; bill length from base of skull: 12.4 mm; bill depth at anterior edge of nares: 3.35 mm; bill width at anterior edge of nares: 3.7 mm; mass 12.0 g (measured with Pesola) and light fat. Skull was 60% ossified, Bursa of Fabricius was absent, and testes measured 7 x 3 mm (left) and 5 x 3 mm (right). The holotype shows no signs of molt and is in fresh plumage. The stomach content included remains of insect larvae, Hymenoptera, and spiders.

Paratype. ICN 35903, subadult male, from Bosque Guayabito, Amalfi, Department of Antioquia, Colombia (6°52'N, 75°36'W; 1825 m elevation); collected and prepared by A.M.C. (field number 713) on 4 January 2005 (see Fig. 1). Differs from holotype in having more extensive pale gray speckling on lores and faint brownish shaft-streaks on anterior forehead. The tips of its rectrices have more indistinct, narrower (ca. 0.3 mm) dull buffy margins. Auriculars show distinct whitish shafts, and the streaking on the throat is more extensive and slightly more distinct (the feathers with narrower whitish areas medially and broader gray lateral borders). Breast band, narrower and less distinct than in the holotype, is pale brownish-gray (near Smoke Gray 45) and its posterior edge is blurred by indistinct pale brownish-gray and yellowish-white streaking on the lower breast and upper abdomen and sides, passing to clear yellow (much paler than Pale Sulphur Yellow 157) on the lower abdomen (Fig. 7). Soft parts as follows: iris bright brownish-red; bill black, base of mandible gray; legs and feet dark gray, black nails and yellowish soles. Wing length: 59.6 mm; tail at the insertion of central rectrices to the tip: 50.4 mm; tarsus: 14.0 mm; bill length from anterior edge of nares: 6.6 mm; bill length at base of skull: 11.4 mm; bill depth at anterior edge of nares: 3.3 mm; bill width at anterior edge of nares: 3.57 mm; mass 10.5 g, with moderate fat. Skull was 80% ossified (Bursa of Fabricius not examined), and left testes measured 3.4 x 2.5 mm. The paratype is in fairly fresh plumage. Stomach contents included insect remains (elytra, pronota). Differences from the holotype are likely due to either age or feather wear; despite its relatively more ossified skull, the paratype male appeared younger in plumage than the adult holotype male, which had no Bursa of Fabricius and showed enlarged testes. Ossification in this genus is often delayed.

Primary formula in the type series. P7-P8-P9 are the longest, nearly the same length; P6 1.2 mm (holotype) to 1.3 mm (paratype) shorter; P10 4.6 mm shorter (holotype) or 4.1 mm shorter (paratype); P5 5.7 mm shorter in both, thus P10 longer than P5 but shorter than P6 (7=8=9>6>10>5).

Etymology. The epithet honors the late Paul Coopmans (1967–2007) in recognition of his acute talent for recognizing bird vocalizations in the field and his knowledge of Neotropical birds. Coopmans made many important discoveries using his extraordinary identification skills by ear (see Krabbe 2008), including *Myiopagis*

olallai, *Scytalopus unicolor*, *Henicorhina negreti*, and an unnamed *Megascops* screech-owl from Sierra Nevada de Santa Marta, Colombia.



FIGURE 7. Dorsal (top), ventral (middle), and lateral (bottom) views of specimens of closely related *Myiopagis* flycatchers of Andean cloud forests. From left to right: “Antioquia *Myiopagis*”: ICN 38437, 35903 (males); *Myiopagis olallai*: MECN 7141 (male), 6902 (male holotype), 7142 (female), 6903 (female paratype), AMNH 819936 (male); “Perijá *Myiopagis*”: COP 6733 (unsexed), Pons 3861 (male), 3860 (female).

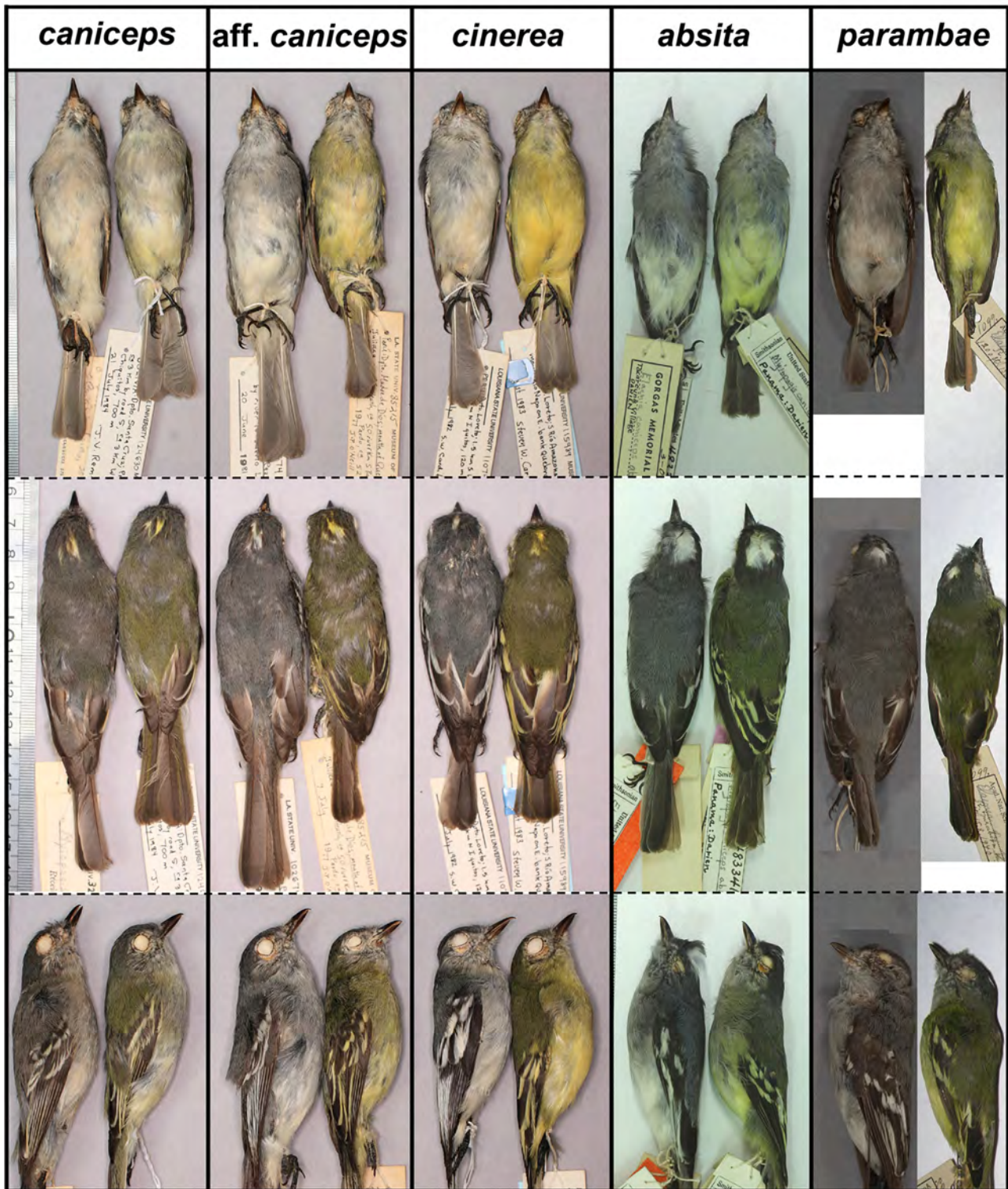


FIGURE 8. Male (left) and female (right) specimens of differentiated lineages of the paraphyletic *Myiopagis caniceps*. From left to right: *M. caniceps caniceps*: LSUMZ 32295, 124630; *M. c. aff. caniceps*: LSUMZ 102674, 85215; *M. c. cinerea*: LSUMZ 110744, 115989; *M. c. absita*: USNM 483342, 483341 (types); *M. c. parambae*: AMNH 499606 (holotype), ANSP 147150 (female). For further information, see Appendix 1.



FIGURE 9. Spread left wing from the holotype of *Myiopagis olallai coopmansii* (ICN 38437).

***Myiopagis olallai incognita*, taxon novum**

Holotype. An adult male deposited in the Adolfo Pons ornithological collection, Caracas (Pons 3861) from Ayapa (=La Sabana), upper Río Negro, State of Zulia, Venezuela (ca. 10°02'N, 72°45'W; 1100 m elevation); collected by M. Nava on 18 August 1951.

Diagnosis. A flycatcher of the genus *Myiopagis*, similar to *M. o. olallai* and *M. o. coopmansii* in morphometrics (Table 3) and the color and pattern of the pileum and crown patch, nape, dorsum and wing markings. Distinguished from nominate *olallai* by its pale gray, rather than bright yellow, underparts, and its pale grayish-olive breast with no hint of olive wash. Although it is more similar to *coopmansii*, it is distinguished from this taxon by its unmarked pale gray throat and more uniform underparts, brighter pale yellow posterior underparts and flanks, paler gray pileum, and duller green upperparts (Fig. 7). Bill tends to be thicker in *M. o. incognita* than in *coopmansii* or *M. o. olallai* (Table 3). The sexes are similar, as in *olallai* and unlike *M. caniceps* (Fig. 8).

Description of holotype. Forehead, crown and nape are neutral gray (Dark Neutral Gray 83), and the midcrown exhibits a large, semi-concealed white patch formed by white feathers with dark gray tips (Black Neutral Gray 82). Back is olive green (Auxiliary Olive Green 47) shading to a slightly lighter tone on rump and upper tail-coverts (Olive Green 46). Rectrices are olive brown dorsally including the rachises (Olive Brown 28), olive green on lateral margins (Bunting Green 150), and show narrow (ca. 0.5 mm) pale yellow tips (lighter than Cream Color 54). Undersides of rectrices are light gray overall (near Glaucous 79) but darker towards the tip, whereas rachises are whitish. Wings are mostly olive brown with slightly darker (near Olive Brown 28) upper wing coverts, and exhibit three narrow but sharply defined pale yellow bars (Pale Sulphur Yellow 157). The width of the proximal two bars ranges between 1–1.5 mm, whereas that of the distal bar (greater coverts) is 1 mm. Primaries are brownish (Olive Brown 28) with a fine olive green edge on the outer webs, and secondaries and tertiaries are olive brown with the edge of outer webs and tips pale yellow (Pale Sulphur Yellow 157). Under wing coverts are pale yellow (Pale Sulphur Yellow 157) and the wrist is brownish dark gray (Vandyke Brown 221). Throat is unmarked and pale gray (near Light Smoke Gray 44), and the breast is light glaucous (Glaucous 80), transitioning smoothly to pale yellow (Pale Sulphur Yellow 157) on flanks and the middle and posterior abdomen. Eye-ring feathers are white, cheeks are

TABLE 3. Mean (\pm standard deviation) morphometric measurements (mm) and body mass (g) of taxa in the *Myiopagis olallai-caniceps* group. Sample sizes are indicated in parentheses. Data from *M. caniceps absita* and *M. c. parambae* were taken from the literature (Hellmayr 1904; 1911; Wetmore 1963).

Taxon	Culmen ^a	Bill length ^b	Bill width ^c	Bill height ^c	Wing	Tail	Tarsus	Mass (g)
Males								
<i>olallai</i>	12.3 (1)	6.9 \pm 0 (3)	3.6 \pm 0.2 (3)	3.3 \pm 0.2 (3)	60 \pm 1 (3)	50.8 \pm 2.3 (3)	16 \pm 1.2 (3)	12.6 \pm 2.1 (2)
<i>coopmansii</i>	11.9 \pm 0.7 (2)	6.8 \pm 0.2 (2)	3.6 \pm 0.1 (2)	3.3 \pm 0 (2)	60.5 \pm 1.3 (2)	50.8 \pm 0.6 (2)	15.1 \pm 1.6 (2)	11.3 \pm 1.1 (2)
<i>incognita</i>	12.3 (1)	7.6 (1)	3.9 (1)	3.3 (1)	59.5 (1)	52 (1)	16.3 (1)	
<i>cinerea</i>	12.1 \pm 0.9 (17)	7.2 \pm 0.4 (17)	3.6 \pm 0.4 (16)	3.3 \pm 0.2 (15)	59.8 \pm 2 (17)	49.9 \pm 2.9 (17)	15.6 \pm 0.7 (14)	10.6 \pm 0.4 (3)
<i>caniceps</i>	12.1 \pm 0.7 (15)	6.6 \pm 0.3 (15)	3.4 \pm 0.3 (15)	3.3 \pm 0.2 (14)	62.1 \pm 1.8 (15)	53.1 \pm 3.1 (15)	16.0 \pm 1.1 (15)	
aff. <i>caniceps</i>	12.6 \pm 0.4 (2)	7.1 \pm 0.3 (2)	3.8 \pm 0.2 (2)	3.4 \pm 0.2 (2)	62.8 \pm 0.4 (2)	53.6 \pm 1.3 (2)	16.6 \pm 0.4 (2)	12.6 \pm 1.5 (2)
<i>absita</i>	10.5 (1)				58 (1)	49.4 (1)	15.5 (1)	
<i>parambae</i>	9.8 \pm 0.3 (3)				55.3 \pm 1.6 (3)	47 \pm 2.7 (3)		
Females								
<i>olallai</i>		7 \pm 0.1 (2)	3.5 \pm 0.3 (2)	3.4 \pm 0.2 (2)	57.5 \pm 2.1 (2)	47.5 \pm 0.7 (2)	16.5 \pm 0.8 (2)	11.7 \pm 0.5 (2)
<i>incognita</i>	12 (1)	7.7 (1)	4.4 (1)	3.7 (1)	55 (1)	47 (1)	15.7 (1)	
<i>cinerea</i>	11.4 \pm 1.2 (6)	7.2 \pm 0.2 (7)	3.7 \pm 0.3 (7)	3.3 \pm 0.2 (6)	55.2 \pm 1.7 (7)	45 \pm 2.5 (7)	14.8 \pm 0.9 (7)	11 (1)
<i>caniceps</i>	11.9 \pm 0.7 (7)	6.4 \pm 0.3 (7)	3.5 \pm 0.3 (7)	3.2 \pm 0.1 (7)	58 \pm 4.2 (7)	47.7 \pm 2.3 (7)	14.7 \pm 0.9 (7)	11.5 (1)
aff. <i>caniceps</i>	11.7 (1)	6.5 (1)	3.1 (1)	3.4 (1)	52 (1)	41.3 (1)	14.7 (1)	
<i>absita</i>	10.2 (1)				52.5 (1)	42.8 (1)	15.6 (1)	
<i>parambae</i>								
Unsexed individuals								
<i>incognita</i> (COP 6733)	11.3	7.4	3.7	3.6	57	49	16.0	
<i>cinerea</i> (COP 22695)	11.4	7.6	3.1	3.6	61	52	16.5	
<i>cinerea</i> (COP 6733)	10.1	6.7	3.2	3.7	63	51	15.9	

^a Total culmen from base of bill at skull to bill tip.

^b Length from anterior edge of nares to bill tip.

^c Taken at anterior edge of nares.

mottled white and gray (Black Neutral Gray 82), whereas the lores and sides of the maxilla base are whitish (near Pale Neutral Gray 86). Soft parts from the label as follows: iris brown (“marrón”); bill and feet brownish gray (“pardo”). Wing length: 59.5 mm; tail at the insertion of central rectrices to the tip: 52 mm; tarsus: 16.3 mm; bill length from anterior edge of nares: 7.6 mm; bill length at base of skull: 12.3 mm; bill depth at anterior edge of nares: 3.3 mm; bill width at anterior edge of nares: 3.91 mm; enlarged testes; in fresh plumage, molt on P8.

Paratypes. (a) An unsexed individual in the Colección Ornitológica Phelps, Caracas (COP 6733) collected on 22 February 1940 by W. H. Phelps at La Sabana (=Ayapa), State of Zulia, Venezuela (ca. 10°02'N, 72°45'W; 1200 m elevation). This specimen was suggested by its collector (Phelps 1943) to possibly represent an immature male on the basis of its green upperparts, as in labeled immature males of the Amazonian taxon *M. caniceps cinerea*, in which adult males have gray upperparts. (b) An adult female in the Adolfo Pons ornithological collection, Caracas (Pons 3860) collected by M. Nava on 18 August 1951 at the type locality (1100 m elevation). The two paratype specimens and the holotype are quite uniform in coloration (Fig. 7).

Primary formula in the type series. In *M. olallai incognita*, P7-P8-P9 are the longest, nearly the same length, and P5 the shortest; P10 shorter than P6 (7=8=9>6>10>5).

Etymology. The feminine Latin word *incognita* means “unknown” or “untested”, and refers to the lack of recognition of this Perijá *Myiopagis* as a species distinct from *M. caniceps* (see Phelps 1943; Ginés *et al.* 1953) for over 70 years. The *incognita* specimens were not examined in the description of *M. olallai* (Coopmans & Krabbe 2000), and have been traditionally treated as vagrant individuals of *M. caniceps*. The name also indicates that this bird remains unknown in life.

Juvenile plumages and color morphs. Juvenile or immature individuals of *M. caniceps cinerea* (e.g. COP 39569, COP 47491) are intermediate to varying degrees between the adult male and the female plumage. The unsexed individual of that taxon (COP 47491) apparently was at an earlier stage of molt to the definitive male plumage. In both these immature specimens, the crown, nape and back are gray with some grayish-olive feathers; the crown patch is white but some feathers have dark gray tips, others grayish-olive tips; the belly, vent and wing markings are mixed pale yellow and white, the flanks olive gray or mixed yellow and gray. This variation in plumage likely led to the suggestion that *M. caniceps* has gray, green, and yellow morphs or “phases” in the males (e.g., Ginés *et al.* 1953; Restall *et al.* 2007). This supposition may have prevented an earlier recognition of the Perijá population (*M. olallai incognita*) as a distinct taxon from the sexually dimorphic *M. caniceps*. In particular, because the first specimen of *M. olallai incognita* (from 1940), which shows the diagnostic green upperparts of *M. olallai*, was initially considered an immature individual of *M. caniceps* due to its external appearance, it was considered to be an intermediate between the preconceived gray and green “typical phases” of *M. caniceps* (Phelps 1943). Nonetheless, Ginés *et al.* (1953) hypothesized that the Perijá population represented a taxon distinct from *M. caniceps* upon observing that the other two sexed adult specimens (from 1951) agreed well with the 1940 specimen that was identified as a juvenile by Phelps (1943), and that the three differed notably from specimens of *M. caniceps* (as described above). The green morph of *M. caniceps* illustrated in Restall *et al.* (2007, p. 393) was based on photographs and specimens of *coopmansii/incognita*.

Discussion

The two distinct *Myiopagis* flycatchers described from the Northern Andes are part of the *M. caniceps-olallai* group. Both resemble superficially the adult female coloration of the southern *M. caniceps caniceps*. Moreover, specimens of *incognita* were heretofore considered vagrant individuals of *M. caniceps* in the green plumage morph (Phelps 1943; Ginés *et al.* 1953; Restall *et al.* 2007). However, both *coopmansii* (Antioquia) and *incognita* (Perijá) share characteristics that are diagnostic of *M. olallai* of the Andean foothills of Ecuador and Peru. For instance, these three taxa are characterized by three pale yellow wing bars, green backs, and gray crowns with a white patch, and mid-elevation cloud-forest habitat of the tropical Andes. Furthermore, songs of *coopmansii* resemble songs of *olallai* but differ in having a much faster pace. Taken together, the striking phenotypic differences and the phylogenetic, vocal and distributional information warrant recognition of *coopmansii* and *incognita*, for which we propose subspecies rank.

Geographic variation and taxonomy of *Myiopagis olallai*. As in nominate *olallai*, the songs of *coopmansii* (unknown in *incognita*) are decidedly divergent from those of *M. caniceps* (see Coopmans & Krabbe 2000). In

contrast, vocalizations of *coopmansii* are reminiscent of those of *olallai* in note shape and song structure. Songs of *coopmansii* seem to differ from typical *olallai* most notably in their faster, longer trills and overall higher pitch. More sound recordings will be necessary to better characterize the vocal repertoire and differentiation of *olallai*, *coopmansii* and *incognita*. During non-systematic playback trials, we observed that individuals of *coopmansii* responded to pre-recorded songs of *olallai* from Ecuador by means of antagonistic behaviors, including agitated vocalizations.

In external morphology, the diagnostic yellow coloration of *olallai* could be misleading regarding the affinities of the newly described taxa, which are predominantly gray below. In spite of this, *coopmansii* and *incognita* are most similar to *olallai* in lacking sexual dichromatism, olive green upperparts, gray head with white coronal patch, whitish throat, and three pale yellow wing bars. In contrast, all known forms of *M. caniceps* are sexually dichromatic, with males mostly having gray upperparts and prominent white wing bars, and females green instead of gray heads. The evolutionary basis of transition from ancestral dichromatism to monochromatism is not well understood, but it is thought to be more common during the speciation of isolated small populations (Badyaev & Hill 2003).

In agreement with the vocal and plumage patterns, genetic differentiation between *coopmansii* and *olallai* is small. Although only two specimens have been sequenced for each of these and none for *incognita*, and nuclear data are not available for *olallai*, our analyses recovered *coopmansii* and *olallai* as a strongly supported clade that was sister to southern populations of *M. caniceps* (including *M. c. caniceps*). Genetic differentiation between some *M. caniceps* taxa was equivalent to the divergence among species in the genus, and these taxa do not form a monophyletic group (also see Rheindt *et al.* 2009). We found that *M. caniceps* is paraphyletic with respect to the Andean *M. olallai* (including *coopmansii*), given the phylogenetic position of *M. caniceps parambae* (of lowland Chocó) and *M. caniceps cinerea* (of northern and western Amazonia). The basal nodes in our trees are not strongly supported, conferring uncertainty to the phylogenetic position of *parambae* and *cinerea* with respect to each other, and to the clade formed by *olallai-coopmansii* and nominal *caniceps*. The subspecies *M. caniceps absita* (of the Canal Zone and Darién, Panama) has not been sequenced, and thus the degree of genetic divergence from *parambae*, its presumed closest taxon, remains unknown.

One interpretation of the available evidence is that it does not satisfy recognizing *coopmansii* or *incognita* as specifically distinct from *M. olallai* under the biological species concept. These three Andean taxa are allopatric, occurring in disjunct Andean ranges and slopes (Fig. 10). Alternatively, the combined divergence in various characters might reflect sufficient evolutionary isolation as to recognize each as separate species. In any case, these provisional interpretations and previous studies (Coopmans & Krabbe 2000; Rheindt *et al.* 2009) do not question the species rank of *M. olallai* under any species concept. Instead, our study suggests the need for formally testing the taxonomic status quo for *M. caniceps*, a species composed of paraphyletic lineages that diverge in evolutionary history (Fig. 6), and morphology (Fig. 8), and seem to differ in vocalizations (Figs. 2, 4). The subspecies *cinerea* and *parambae* may prove to represent species-level taxa when studied in depth. Insights should be gained from quantitative study of vocalizations with vouchered specimens, range-wide phylogeographic and ecological studies, museum work to characterize phenotypic variation, and fieldwork to delineate distribution boundaries among *M. caniceps* taxa.

Distribution and ecology. *Myiopagis olallai* is an elusive, inconspicuous inhabitant of the canopy of foothill and lower montane forests, and remains one of the least known species in the Tyrannidae (Coopmans & Krabbe 2000). Our results suggest that *M. olallai* has a larger geographic range than previously thought, but it is highly discontinuous along the Andes (Fig. 10), extending to the northern end of the Central Cordillera of Colombia and possibly Serranía de San Lucas (as *M. o. coopmansii*), and the Serranía de Perijá in Venezuela (as *M. o. incognita*). The five previously known specimens of the nominate subspecies are from a handful of highly disjunct localities along the eastern slope of the Andes between Napo, Ecuador, and Apurímac, Peru (Coopmans & Krabbe 2000). The species has subsequently been found in various localities in central Peru (Pasco and Junín) filling part of the geographic gap along the eastern slope of the Andes (sound recordings and photographs by A. García, D. Geale, W-P. Velinga, and D. F. Lane; see Appendix 2). Although we did not detect consistent differences between Ecuadorian and Peruvian recordings, the southern populations are the least known along with *incognita* of Perijá. To the north, the yellowish form of *M. olallai* occurs as far north as Serranía de Cofán in Sucumbíos, Ecuador, less than 10 km from the Colombian border (T. S. Shulenberg in Pitman *et al.* 2002). Therefore, the distribution of nominate *olallai* may include the Amazonian slope of the Colombian Andes.

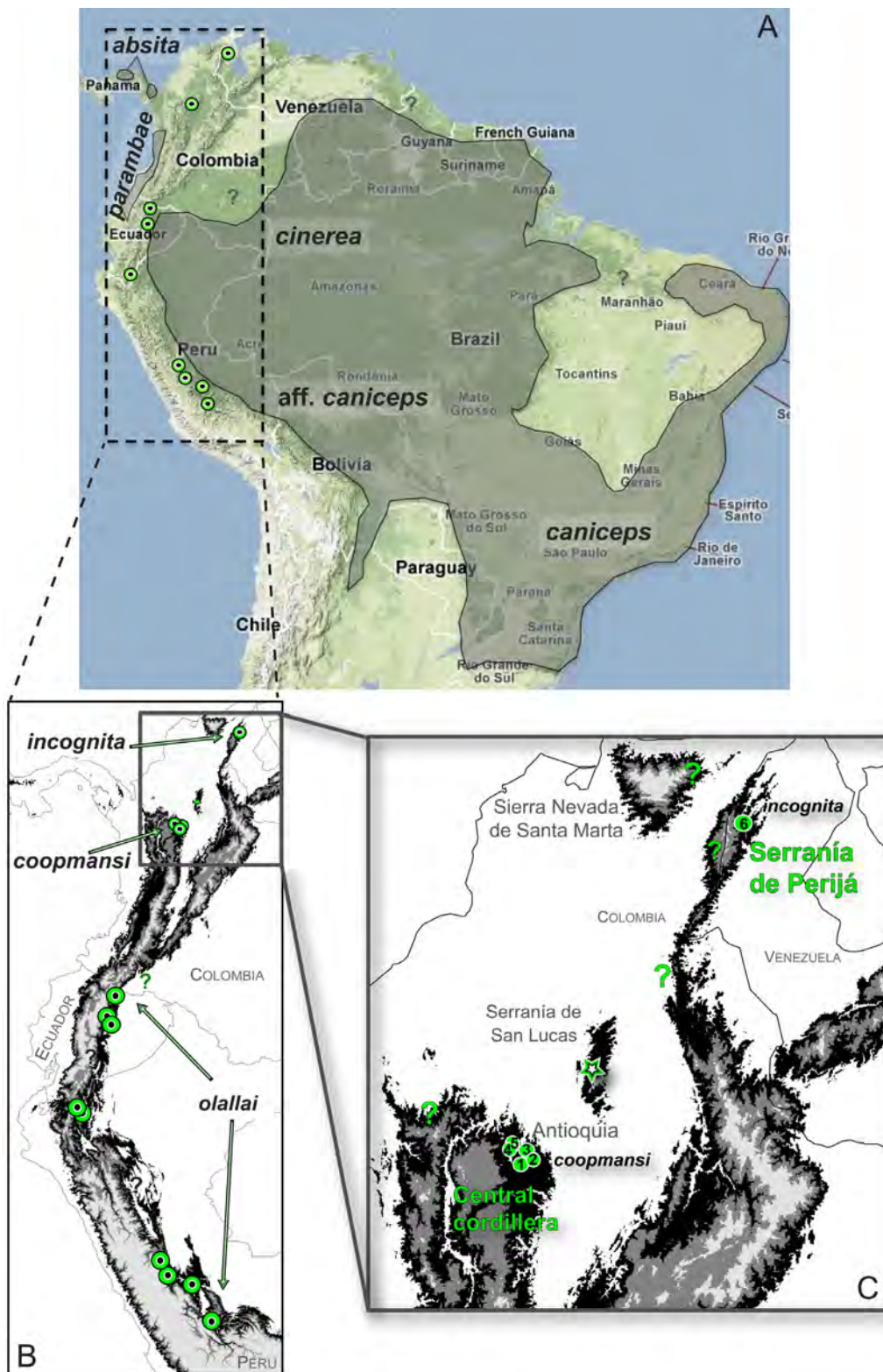


FIGURE 10. Geographical distribution of *Myiopagis caniceps* (shaded area) and *M. olallai* (green dots). (A) Approximate distribution of differentiated lineages in *M. caniceps*. (B) Inset map showing the locality records of *M. olallai* along the Andes, including the Antioquia (*coopmansii*) and Perijá (*incognita*) forms. (C) Detailed map of the northern Andes in Colombia and western Venezuela showing the localities of *M. olallai coopmansii* in the northern Central cordillera, Antioquia, Colombia (1: Bosque Guayabito, 2: Bosque Las Ánimas, 3: Bodega Vieja, 4: La Forzosa, 5: Alto El Chaquiral), and of *M. olallai incognita* in the Serranía de Perijá (6: Ayapa). For details on localities see text and Cuervo *et al.* (2008a). Question marks are placed at sampling gaps in the range of this group of *Myiopagis*, where future fieldwork could confirm the occurrence of these taxa. The star at Serranía de San Lucas indicates misidentified sound recordings (XC92160, XC104264, XC104475) that do appear to correspond to *M. o. coopmansii*, but this locality needs specimen confirmation.

All field observations of *M. o. coopmansii* involved birds in mixed-species flocks foraging high in the tall canopy of primary cloud forests. The northern end of the Central Cordillera is a biogeographic hotspot where lineages of multiple biogeographic origins occur and endemic bird species like *Lipaugus weberi* are threatened (Cuervo *et al.* 2008a). The range of the newly discovered *M. o. coopmansii* might include the least explored adjacent areas of the northernmost Western Cordillera, which have suitable habitat for this taxon within its known elevational range (Fig. 10). In Serranía de Perijá, *M. o. incognita* is only known from the type series collected on the eastern slope in Venezuela, where a national park protects continuous tracts of cloud forest habitat. This bird has not been recorded since 1951; recent field work in the Colombian slope concentrated on elevations above the known records of this taxon (López-O. *et al.* 2014). Although it may well extend to the Colombian side of Perijá, vast deforestation along the west slope has left only very small habitat patches. The habitat is cleared below 1,600 m in most areas (López-O. *et al.* 2014). This enigmatic taxon might also occur in Sierra de Ocaña and the Sierra Nevada de Santa Marta.

The elevational range of *M. olallai* in Ecuador and Peru is 900–1,500 m (Coopmans & Krabbe 2000; Schulenberg & Kirwan 2012), whereas *M. o. coopmansii* occurs at slightly higher elevations, from 1,300 up to 1,850 m. The three specimens of *M. o. incognita* were taken between 1,100 and 1,200 m in Perijá. All known records of *M. olallai* occur entirely above the upper elevational limit of the distantly related *M. caniceps cinerea* (<700 m; Schulenberg & Kirwan 2012), the only *caniceps* taxon with which *M. olallai* could overlap along the Amazonian slopes from Ecuador through central Peru. The sister clade of *M. olallai* ranges as close as southern Peru (*M. c.* aff. *caniceps*) in the Amazonian lowlands and foothills of Puno, but *M. olallai* has not been recorded that far south. *Myiopagis olallai* may be one example of adaptation by an Atlantic forest ancestor to novel Andean environments, and rapid plumage evolution in geographic isolation.

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APPENDIX 1. Museum specimens of *Myiopagis caniceps* and *Myiopagis olallai* examined.

Museum acronyms as follows: American Museum of Natural History, New York (AMNH); Academy of Natural Sciences of Philadelphia (ANSP); Colección Ornitológica Phelps, Caracas (COP); Centro de Ornitología y Biodiversidad, Lima (CORBIDI); Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá (ICN); Museum of Natural Science, Louisiana State University, Baton Rouge (LSUMZ); Museo Ecuatoriano de Ciencias Naturales, Quito (MECN); Moore Laboratory of Zoology, Los Angeles (MLZ); Colección Adolfo Pons, Caracas (Pons); Senckenberg Museum, Frankfurt (SMF); National Museum of Natural History, Smithsonian Institution, Washington, D. C. (USNM); Zoologische Staatssammlung München (ZSM). Sex is given in parenthesis. Asterisks denote sequenced individuals (see Table 1).

- M. caniceps caniceps***: BRAZIL, Bahia central, Oroba: AMNH 243899 (female); Bahia central/oriental, Jaguaguara: AMNH 243900 (male); Matto Grosso, Chapada: AMNH 3334 (male); Paraná, Foz do Iguaçú: AMNH 318871 (female), AMNH 318867 (male); Vitoria, E Sao Paulo: AMNH 499601 (female); Goiás, Goiânia: LSUMZ 32295 (male). ARGENTINA, Misiones, Arroyo Uruguayo: AMNH 772697 (female), AMNH 772692 (male), AMNH 772690 (male), LSUMZ 56700 (male), LSUMZ 56701 (male), LSUMZ 56702 (male); Misiones, Tobunás: MLZ 65635 (male), MLZ 65636 (female), MLZ 65637 (male); PARAGUAY, East of Villa Rica: AMNH 320132 (female); Ipame River: AMNH 319805 (male), AMNH 319804 (male); Northern La Fonciere, San Luis de la Sierra: AMNH 321121 (male); BOLIVIA, Santa Cruz, 3 km W Santiago by road: LSUMZ 124630* (B6656) (female).
- M. caniceps* aff. *caniceps***: BOLIVIA, La Paz, Río Beni, 20 km by river N Pto. Linares: LSUMZ 102674* (B1048) (male). PERU, Puno, 25 km NE San Juan de Oro: LSUMZ 179667* (B58379) (male), CORBIDI DFL2288* (female); Madre de Dios, mouth of Quebrada Juliaca on Río Heath: LSUMZ 85215 (female).
- M. caniceps cinerea***: VENEZUELA, Solano, Río Casiquiare, left bank: AMNH 433187 (male), AMNH 433189 (male); Suapure, Orinoco: AMNH 499605 (male); Campamento El Trueno, Río Caura: COP 70032 (female); Sabana de Alto Río Asisa: COP 47491 (unsexed), COP 47492 (male), COP 47506 (male), COP 47507 (female), COP 47508 (female); Pica Yavita-Pimichín, Campamento La Cruz: COP 34650 (male); Las Carmelitas, Río Ventuari: COP 38704 (male); Puerto Yapacana: COP 39569 (male); Puerto Carretico, Cerro Mato: COP 53269 (female); Río Tonoro, Río Paragua: COP 22695 (unsexed); Salto El Payaso, Río Paragua: COP 30279 (male); Salto Guaiquinima, Río Paragua: COP 30282 (female), COP 30278 (male); Caño Piedra, Caño Cuao: COP 33690 (male); Atures, Caño Cataniapo: COP 21019a (male). BRAZIL, Rio Vaupés, left bank, Iguararé: AMNH 434805 (female); COLOMBIA, Río Huaynia junction with the Casiquiare, right bank: AMNH 433188 (male); “Bogotá”: SMF 42116 (unsexed juvenile, likely a male by plumage), SMF 42117 (male). PERU, Amazonas, 4 km SW Chiriaco: LSUMZ 64399 (male); Loreto, ca. 54 km NNW mouth of Río Morona: LSUMZ 173017 (male); Loreto, ca. 10 km SSW mouth of Río Napo on E bank Quebrada Vainilla: LSUMZ 115989 (female); Loreto, 1.5 km S Libertad, S bank Río Napo, 80 km N Iquitos: LSUMZ 110744 (male); Ucayali, Yarinacocha: LSUMZ 71334 (male).
- M. caniceps parambae***: ECUADOR: Esmeraldas, Paramba: AMNH 499606 (male holotype). COLOMBIA: Chocó, Nuquí, Río Jurubidá: ANSP 146915 (male, immature?), ANSP 147149 (male, immature?), ANSP 147150 (female); Chocó, Noanamá, Río San Juan: ZSM 2196 (male, juvenile); Chocó, Novitá, Río Tamaná: ZSM 2196 (male, immature?).
- M. caniceps absita***: PANAMA: Darién, Tacarcuna Village, headwaters of Río Pucro, base of Cerro Mali: USNM 483342 (male holotype), USNM 483341 (female paratype).
- M. olallai olallai***: ECUADOR: Zamora-Chinchipec, 5 km SE Zamora, Río Bombuscaro: MECN 6902 (male holotype), MECN 6903 (female paratype); Napo: km 35 vía Loreto: MECN 7141 (male), MECN 7142 (female). PERU: Cusco, Cordillera de Vilcabamba, 6 km E of Luisiana: AMNH 819936 (male).
- M. olallai coopmansii* ssp. nov.**: COLOMBIA: Antioquia, Amalfi, Bodega Vieja: ICN38437* (male holotype); Antioquia, Amalfi, Bosque Guayabito: ICN 35903* (male paratype).
- M. olallai incognita* ssp. nov.**: VENEZUELA: Zulia, Serranía de Perijá, Ayapa (=La Sabana): COP 6733 (unsexed paratype), Pons 3861 (male holotype), Pons 3860 (female paratype).

APPENDIX 2. Sound recordings of *Myiopagis olallai* examined. Recordings by N. Krabbe and J. Nilsson taken from Lysinger *et al.* (2005) and Krabbe & Nilsson (2007), and those by M. G. Harvey from ML.

Recording	Recordists (Date)	Locality (elevation above sea level in meters)
<i>Myiopagis olallai olallai</i>		
K4	N. Krabbe (3-Nov-90)	Ecuador: Napo, Pan de Azúcar (1200)
K1	J. Nilsson (16-Jul-02)	Ecuador: Napo, km 53 Narupa-Loreto rd (1260)
Lys 2 (K2)	N. Krabbe (26-Aug-96)	Ecuador: Napo, km 53 Narupa-Loreto rd (1260)
Lys 5 (K5)	N. Krabbe (17-Dec-96)	Ecuador: Napo, km 35 Narupa-Loreto rd (1080)
XC 3509	N. Athanas (23-Jun-03)	Ecuador: Napo, Loreto Road (1150)
XC 70742-70745	A. Spencer (26-Jan-11)	Ecuador: Napo, Wildsumaco, 5km NW Guagua Sumaco (1450)
XC 97992-97993	T. Brooks (26-Jan-11)	Ecuador: Napo, Wildsumaco, 5km NW Guagua Sumaco (1450)
K3	N. Krabbe (28-Jan-02)	Ecuador: Morona-Santiago, Cordillera de Cutucú (1000)
ML 60232	P. Coopmans (20-Jun-92)	Ecuador: Zamora-Chinchiipe, Bombuscaro, Podocarpus NP (1050)
K 6 - K 8	N. Krabbe (31-Aug-92)	Ecuador: Zamora-Chinchiipe, Río Bombuscaro (1000)
XC 62220	W.-P. Vellinga & A. Garcia (24-Aug-10)	Peru: Pasco, Pan de Azúcar, sector Huampal (1000)
XC 61012-61013	D. Geale (18-Jul-10)	Peru: Pasco, Villa Rica area (1650)
XC 105085-105087	D. F. Lane (24-Jun-12)	Peru: Junín, Ridge NE of Puerto Ocopa (1350)
<i>Myiopagis olallai coopmansii</i>		
IAvH-BSA 19066	A. M. Cuervo (2-Jul-02)	Colombia: Antioquia, Amalfi, Bodega Vieja (1525)
IAvH-BSA 19077	A. M. Cuervo (9-Jul-02)	Colombia: Antioquia, Amalfi, Bodega Vieja (1525)
IAvH-BSA 19543	A. M. Cuervo (21-Jan-02)	Colombia: Antioquia, Amalfi, Bosque Guayabito (1720)
IAvH-BSA 19551-19552	A. M. Cuervo (21-Jan-02)	Colombia: Antioquia, Amalfi, Bosque Guayabito (1700)
IAvH-BSA 19569	A. M. Cuervo (23-Jan-02)	Colombia: Antioquia, Amalfi, Bosque Guayabito (1750)
IAvH-BSA 19580	A. M. Cuervo (24-Jan-02)	Colombia: Antioquia, Amalfi, Bosque Guayabito (1750)
IAvH-BSA 19585	A. M. Cuervo (9-May-06)	Colombia: Antioquia, Amalfi, Bosque Guayabito (1835)
MGH 085-086	M. G. Harvey (19-Jan-14)	Colombia: Antioquia, Amalfi, Bosque Guayabito (1740)
IAvH-BSA 19187	A. M. Cuervo (8-Feb-02)	Colombia: Antioquia, Amalfi, Bosque Las Animas (1540)
IAvH-BSA 19217-19218	A. M. Cuervo (11-Feb-02)	Colombia: Antioquia, Amalfi, Bosque Las Animas (1540)
IAvH-BSA 19401	A. M. Cuervo (20-Mar-02)	Colombia: Antioquia, Anorí, Alto El Chaquiral (1665)
IAvH-BSA 19832	A. M. Cuervo (24-May-99)	Colombia: Antioquia, Anorí, La Forzosa (1550)
IAvH-BSA 19941	A. M. Cuervo (21-Dec-99)	Colombia: Antioquia, Anorí, La Forzosa (1780)