A new subspecies of Common Bush-Tanager *(Chlorospingus flavopectus*, Emberizidae) from the east slope of the Andes of Colombia

Una nueva subespecie de Montero Común *(Chlorospingus flavopectus*, Emberizidae) de la vertiente oriental de los Andes de Colombia

Jorge Enrique Avendaño[1,2], F. Gary Stiles[3] & Carlos Daniel Cadena[1]

[1]Laboratorio de Biología Evolutiva de Vertebrados, Departamento de Ciencias Biológicas, Universidad de los Andes, A.A. 4976, Bogotá, Colombia.
[2]Current address: Programa de Biología y Museo de Historia Natural, Universidad de los Llanos, Sede Barcelona, Villavicencio, Colombia.
[3]Instituto de Ciencias Naturales, Universidad Nacional de Colombia, A.A. 7495, Bogotá, Colombia.
✉ jorgeavec@gmail.com, fgstilesh@unal.edu.co, ccadena@uniandes.edu.co

Abstract

We describe *Chlorospingus flavopectus olsoni*, subsp. nov. from the east slope of the Eastern Andes of Colombia. Specimens from the range of the new subspecies have been traditionally referred to *C. f. macarenae*, a subspecies endemic to the Serranía de la Macarena. However, *C. f. olsoni* differs from *C. f. macarenae* in plumage, iris coloration, and morphometrics. The new subspecies is more similar in plumage and vocal characters to subspecies *exitelus* and *nigriceps* from the Central and Eastern Andes. Ecological niche modeling suggests that *C. f. olsoni* is potentially restricted to a small belt of cloud forest south of the Sierra Nevada del Cocuy to the depression known as Las Cruces Pass in the department of Huila. The species *C. flavopectus* is not threatened, but the accelerated deforestation of cloud forests in Colombia and the uncertainty about species limits in the complex call attention to the importance of preserving the remaining patches of this highly species-rich ecosystem.

Key words: Andes, *Chlorospingus flavopectus*, *Chlorospingus ophthalmicus,* cloud forest, Emberizidae, geographic variation, oscine vocalizations, taxonomy.

Resumen

Describimos a *Chlorospingus flavopectus olsoni*, subsp. nov. de la vertiente oriental de la cordillera Oriental de Colombia. Tradicionalmente, los especímenes recolectados en el ámbito de la nueva subespecie han sido asignados a *C. f. macarenae*, una subespecie endémica de la Serranía de la Macarena. No obstante, *C. f. olsoni* difiere en plumaje, coloración del iris y morfometría. Con base en caracteres de plumaje y vocalizaciones, la nueva subespecie es más similar a las subespecies *exitelus* y *nigriceps* de las cordilleras Central y Oriental. Los análisis de modelamiento de nicho sugieren que *C. f. olsoni* está potencialmente restringida a una estrecha franja de bosque de niebla desde el sur de la Sierra Nevada del Cocuy hasta la depresión conocida como el Paso de las Cruces en el departamento del Huila. La especie *C. flavopectus* no está amenazada, aunque la acelerada deforestación de los bosques de niebla en Colombia y la incertidumbre sobre los límites de especies en el complejo hacen un llamado a conservar los últimos remanentes de este ecosistema altamente rico en especies.

Palabras clave: Andes, bosque de niebla, *Chlorospingus flavopectus*, *Chlorospingus ophthalmicus*, Emberizidae, taxonomía, variación geográfica, vocalizaciones de oscines.

Introduction

The Common Bush-Tanager *Chlorospingus flavopectus* (Emberizidae, formerly widely known as *C. ophthalmicus)* represents one of the most geographically variable complexes of Neotropical

cloud forest birds, comprising 25 named subspecies, which vary mainly in plumage characters (Isler 1999, Sánchez-González 2007). The marked geographic variation observed within *C. flavopectus* has been attributed to its restriction to cloud forests, which have a patchy and discontinuous distribution in the Neotropics. Therefore, gene flow may be restricted or impeded between populations, favoring their differentiation (García-Moreno 2004, Sánchez-González 2007). Some authors (*e. g.*, Olson 1983) have suggested that more than one species should be recognized in what may best be referred to as the "*Chlorospingus flavopectus-ophthalmicus* complex". In Colombia, cloud forests are highly fragmented along all three Andean ranges and isolated mountain ranges (Etter 1998, Armenteras *et al.* 2007, Graham *et al.* 2010). Each cordillera has its own set of distinct subspecies in the "*Chlorospingus flavopectus-ophthalmicus* complex", which replace each other on different slopes or latitudinally (Hilty & Brown 1986). In particular, the Eastern Andes, which extend from the Ocaña depression in department of Norte de Santander south to the main Andean range (Macizo Colombiano) in the department of Nariño, exhibit a mosaic of allopatric or parapatric replacements of subspecies along both slopes. On the west slope subspecies *jacqueti*, *trudis*, *flavopectus* and *nigriceps* replace each other from north to south. On the east slope, north-to-south replacements involve *eminens*, *macarenae*, *nigriceps,* and *phaeocephalus* (Fig. 1). This paper focuses on the East Andean population heretofore referred to as *macarenae*.

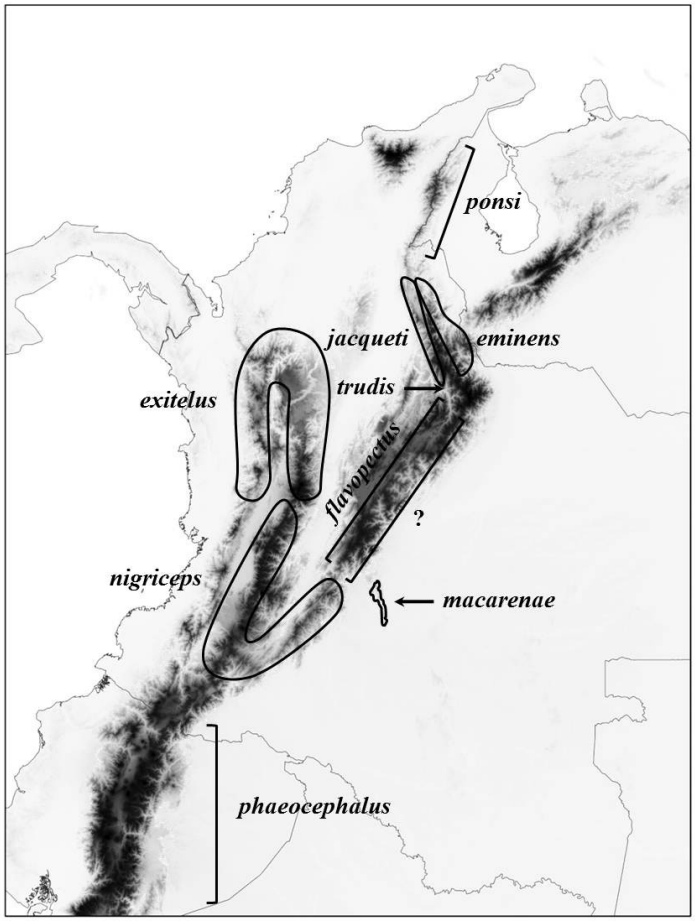

Figure 1. Approximate geographic distributions of nine subspecies of *Chlorospingus flavopectus* in Colombia. The East Andean population outlined with the question mark (?) is the new subspecies described in this paper, which has been traditionally referred to the subspecies *C. f. macarenae*, endemic to the Serranía de la Macarena.

The subspecies *macarenae* was described by Zimmer (1947) as very closely resembling *flavopectus* of the west slope, but apparently restricted to the Serranía de la Macarena, an isolated range east of the Andes in the department of Meta. In October 1967, A. Olivares and P. Bernal collected three *C. flavopectus* from Cerro Comijoque, municipality of Pajarito, department of Boyacá on the eastern slope of the Eastern Andes, the first specimens from this slope south of the Sierra Nevada del Cocuy. Olivares (1971) classified the Pajarito specimens as pertaining to *macarenae*, apparently based upon the differences of these specimens relative to *flavopectus* and the geographical proximity to the range of *macarenae*. Since then, the subspecies ranging from the eastern slope in the departments of Boyacá and Cundinamarca has been uncritically treated as *macarenae*. However, recent field work and collecting conducted by us and others along this slope has permitted a better understanding of the distribution and geographic variation of *C.*

flavopectus in the region. Comparison with topotypical *macarenae* specimens and analyses of morphometrics, dawn songs and ecological niche modeling make it evident that the *"macarenae"* population of the eastern slope in fact represents an undescribed and distinctive new subspecies, which we propose to name:

Chlorospingus flavopectus olsoni, subsp. nov.

Holotype.– Adult male, no. 30940 of the ornithological collection of the Instituto de Ciencias Naturales (ICN), Universidad Nacional de Colombia; collected on 13 January 1991 by F. G. Stiles (original no. FGS-2791) at an elevation of 2050 m (04^{0}16'N, 73^{0}48'W) beside the Monterredondo-El Calvario road, municipality of Guayabetal, c. 3 km ENE of the town of Guayabetal, department of Cundinamarca, Colombia.

Diagnosis.–Most like *C. f. exitelus* from the Central Andes but crown gray, instead dark brownish-gray. It also differs slightly in its dark brown periorbital ring extending below the auriculars, which are light grayish-brown rather than concolor with the crown; the whiskers and speckling on the throat are lighter, the background color of the throat is more yellowish and malar region is buffy rather than whitish. Compared with *macarenae*, *olsoni* is larger, the crown is slightly darker, whiskers are conspicuous and speckling on throat is slight, the latter two characters absent in *macarenae*, and its iris color is yellowish in adults, not brick red. The new subspecies is smaller than *flavopectus* and *trudis* of the western slope of the Eastern Andes, which also differ in their brick red irides; the crown of *olsoni* is slightly darker with contrasting light grayish-brown auriculars, with a browner periorbital area and more speckling on throat, which is buffier. The pectoral band of *olsoni* is more orange than either *flavopectus* and *trudis*; its abdomen is more whitish than in *flavopectus* and more grayish than in *trudis*. The crown of *olsoni* is paler than that of *nigriceps* from the Central and Eastern Andes, and its throat is much less speckled. It also differs from other geographically adjacent subspecies, such as *eminens* (Tamá region) and other subspecies from the Eastern Andes and Venezuela in lacking the white postocular spot and in having the crown gray rather than shades of brown (see Figs. 2-3 for illustrations of most of the Colombian subspecies of this complex).

Figure 2. Some subspecies of *Chlorospingus flavopectus* found in Colombia and Venezuela. (A) *C. f. flavopectus*, vereda San Isidro, Galán, dpto. Santander, (B. Huertas/ Proyecto YARE); (B) *C. f. trudis*, vereda Santa Cruz, San Andrés, dpto. Santander (JEA); (C) *C. f. phaeocephalus*, vereda El Verde, Puerres, dpto. Nariño (C. Flórez); (D) *C. f. olsoni*, Cerro La Rusa, Miraflores, dpto. Boyacá (N. Espejo); (E) *C. f. exitelus*, vereda La Lana, San Pedro de los Milagros, dpto. Antioquia (B. Huertas); (F) *C. f. nigriceps*, Roncesvalles, dpto. Tolima (H. Loaiza); (G) *C. f. ponsi*, vereda El Cinco, Manaure, dpto. Cesar, Colombia (JEA); (H) *C. f. jacqueti*, EBA La Judía, Floridablanca, dpto. Santander (E. Briceño); (I) *C. f. venezuelanus*, Páramos de Batallón y La Negra NP, edo. Táchira, Venezuela (A. M. Cuervo). *C. f. macarenae* is not shown because it has never been photographed alive.

Figure 3. Plumage variation among adult males of *C. f. olsoni* and other Colombian subspecies. From left to right: *C. f. flavopectus* (ICN 36905), Filo Pamplona, Serranía de los Yariguíes, vereda San Isidro, Galán, dpto. Santander; *C. f. macarenae* (MHNUC-A-2739), Pico Renjifo, Serranía de la Macarena, dpto. Meta; *C. f. olsoni* (holotype); *C. f. exitelus* (IAvH 11938), Hacienda Termópilas, Aranzazu, dpto. Caldas; *C. f. nigriceps* (ICN 33446), Serranía de los Churumbelos, Nabú, Finca Playón, vereda Petrólea, Santa Rosa, dpto. Cauca; and *C. f. eminens* (IAvH 12187), sector Sisavita, Cucutilla, dpto. Norte de Santander. Photographs by J. P. López-O.

Description of the holotype.– Capitalized color names and numbers follow Smithe (1975, 1981). Crown and neck Dark Neutral Gray (83), washed with Olive-Brown (28). The periorbital area is between Fuscous (21) and Sepia (219) becoming paler behind the auriculars, which are dark Smoke Gray (44) washed with Light Drab (119C). The back, rump, upper tail coverts, wing coverts, and outer webs of the remiges and rectrices are Citrine (51), tinged with Olive Yellow (52). The inner webs and tips of the remiges and rectrices are Greenish Olive (49) or duller. Throat is white tinged with Buff (124), which is more accentuated in the malar region; the lower throat just above the pectoral band is between Pale Horn Color (92) and Pale Pinkish Buff (121D). Slight throat speckles and whiskers are Natal Brown (219A). The breast band is Spectrum Yellow (55) tinged with Orange-Yellow (18) at the center and with Olive Yellow (52) to the sides. The flanks, legs and undertail coverts are Olive Yellow (52) tinged with Yellowish Olive-Green (50). The abdomen is white, slightly washed with Pale Neutral Gray (86). The iris is dull red in the periphery and whitish near the pupil, giving an overall yellowish appearance; the bill is black, the tarsi and feet gray. The body mass was 20.2 g, the left testis measured 9.0 x 6.5 mm, the skull was completely ossified, and some subcutaneous fat was present. Stomach contents included a homopteran, larvae and adults of coleoptera, and one spider. Measurements (in mm): total culmen 14.0, bill length from anterior edge of nostril 7.6, bill depth at nostril 5.2, bill width at nostril 4.3,

wing chord 66.8, tarsus 21.2, tail 61.5.

Paratypes.– Adult male (ICN 36936) collected above the type locality (2280 m) beside the Monterredondo-El Calvario road on 9 November 2008 by J. E. Avendaño; three additional adult males (ICN 17426, 17428, 25592) and two adult females (ICN 17427, IAvH 3778), all collected on the right margin of the Cusiana River, Hacienda Comijoque, municipality of Pajarito, Department of Boyacá, at an elevation of 2000 m by ICN and IAvH personnel between 1967 and 1980; a female (ICN 38090) collected at 2120 m at vereda Centro Norte, municipality of Chámeza, department of Casanare, by J. Miranda and O. Laverde on 14 July 2010.

Variation in the type series.– Plumage variation is slight and mainly concentrated in the color of the crown and breast band. Male ICN 36936 has a lighter crown (less olive-brown) than the holotype and female ICN 38090, whereas the rest of paratypes are browner (Olive Brown (28)) perhaps due to foxing. The color of the breast band varies from yellow-orange (ICN 17426-27, 38090) as in the holotype to plain yellow (ICN 17428, 25592, 36936). Throat color is slightly variable among individuals, whereas observed variation in speckling coloration could be affected by specimen age. In addition, iris coloration apparently varies with age. In most cases, adults exhibited yellow or orange-yellow irides, and subadults or not fully reproductive individuals had hazel or red eyes. However, two males with enlarged testes (ICN 17426, holotype) had traces of red. No significant sexual dimorphism in morphometrics or plumage coloration exists within the type series.

Etymology.–The subspecies epithet honors Dr. Storrs L. Olson, senior scientist of the Division of Birds of the Smithsonian National Museum of Natural History, for his substantial and ongoing contribution to the study of geographic variation and systematics of extant and extinct Neotropical birds. Particularly, he has studied geographic variation in the *Cholorospingus flavopectus-ophthalmicus* complex, describing two new subspecies from the Central and Eastern Cordilleras of Colombia, and highlighting the importance of continued field work and collecting to resolve species limits in this and other little-studied groups.

Morphometrics.– Although *C. f. olsoni* is readily diagnosable based on plumage characters, we explored possible differences in morphometrics with other Colombian subspecies. Pairwise tests have been proposed to assess the diagnosability of subspecies (Patten & Unitt 2002, Remsen 2010); however, these tests could be biased by small samples ($n \leq 20$-30). Therefore, because of our small sample in some subspecies we applied a conservative approach using *t*-tests with the Bonferroni correction. The appropriate *t* values were determined by $\alpha = 0.0125$ and 0.0025, which respectively result from applying the Bonferroni correction ($\alpha = 0.05$ and 0.01 divided by $K = 4$, where K is the number of variables compared between pairs of populations; see below), and the degrees of freedom ($df_{ij} = n_i + n_j - 2$, where n is the sample size of each subspecies). Although t-tests do not evaluate diagnosability *per se*, they are appropriate for discerning quantitative differences in continuous traits by answering the question of whether two samples (subspecies' trait values) could have been drawn from the same statistical population.

We measured 128 adult males and 73 adult females from ten Colombian subspecies of *C. flavopectus* (Appendices 1 and 2). Preliminary analyses indicated that differences between subspecies occurred mainly in four morphometric variables, which we measured with calipers to the nearest 0.1 mm: length of total culmen (from the

Table 1. Summary of comparisons (*t*-tests) for three morphometrics between males (♂) and females (♀) of *Chlorospingus flavopectus olsoni* and other nine subspecies. ns = p>0.05; * = p≤0.0125; ** = p≤0.0025; / = not calculated. Note that males and/or females of *C. f. olsoni* are distinct from most Colombian subspecies. Culmen total was not included because results were statistically non-significant for all comparisons. Measurements of each morphometric are presented in the Appendix 2.

Subspecies	Tarsus		Tail		Wing chord	
	♂	♀	♂	♀	♂	♀
ponsi	ns	ns	ns	ns	ns	ns
jacqueti	ns	ns	ns	ns	**	ns
eminens	ns	ns	ns	ns	*	ns
flavopectus	**	ns	**	ns	*	ns
trudis	**	ns	ns	ns	ns	ns
exitelus	ns	ns	ns	/	ns	/
nigriceps	ns	ns	ns	ns	ns	ns
macarenae	ns	ns	ns	**	ns	ns
phaeocephalus	ns	ns	ns	*	ns	ns

base to tip), wing chord, tail (from the insertion of the central rectrices to their tip), and tarsus. Although we found no significant sexual dimorphism in morphometrics in *C. f. olsoni* (perhaps due to the small sample size), we conducted tests separately by sex because males are larger in other Colombian subspecies. Our analyses show that *C. f. olsoni* differs in one or more morphometric variables from six out of nine Colombian subspecies (Table 1). Particularly, *C. f. olsoni* is distinguishable from *macarenae* by a longer tail in females, whereas males differ from *flavopectus* in their shorter tarsi, tails and wing chords. Males of *C. f. olsoni* also have longer wings and shorter tails and tarsi than the subspecies *jacqueti*, *eminens* and *trudis*. For a complete characterization of the morphology of the Colombian subspecies, see Appendix 2.

Vocalizations.–Dawn songs are known to differ qualitatively among subspecies of *C. flavopectus* in Colombia (Cadena *et al.* 2007). We could not compare quantitatively the dawn songs of all subspecies of *C. flavopectus* occurring in Colombia because few recordings of voices of most taxa are available, so we describe variation qualitatively. Based on two recordings, the dawn song of *C. f. olsoni* appears more similar in structure, note shape and pitch to those of *nigriceps*, *eminens* and *jacqueti* than to that of *flavopectus*, *trudis* (*trudis* heard by JEA) and phenotypically similar subspecies from Ecuador and Peru (*e.g., C. f. phaeocephalus* and *cinereocephalus)* (Fig. 4). However, one *olsoni* dawn song ends with a fast and high-pitched trill. We are not aware of the presence of this trill in other Colombian subspecies we know well (*i.e. jacqueti* and *ponsi* from the Eastern Andes). A final trill was reported for *nigriceps* in department of Huila, but this trill in fact corresponds to an overlapping call of *Pseudocolaptes boissonneauti* (Cadena *et al.* 2007; Banco de Sonidos Animales-BSA 16656); *macarenae* and *exitelus* are unknown vocally. A complete geographic sampling of dawn songs, particularly in the Eastern Andes, is necessary to explore the magnitude of these preliminary differences observed and to assess their potential role as mechanisms of reproductive isolation.

Distribution.–*C. f. olsoni* is endemic to the east slope of the Eastern Andes, where it is known from seven localities ranging from Cerro Comijoque in Boyacá, south to the Guayabetal-El Calvario road in Cundinamarca. To obtain a more detailed assessment of the potential distribution of this new taxon, we conducted an ecological niche modeling analysis in the program Maxent version 3.3 (Phillips 2006), using 19 climate variables available in the WORLDCLIM ver. 1.2 database (Hijmans *et al.* 2005), and 13 remote-sensing variables related to vegetation and three related to topography

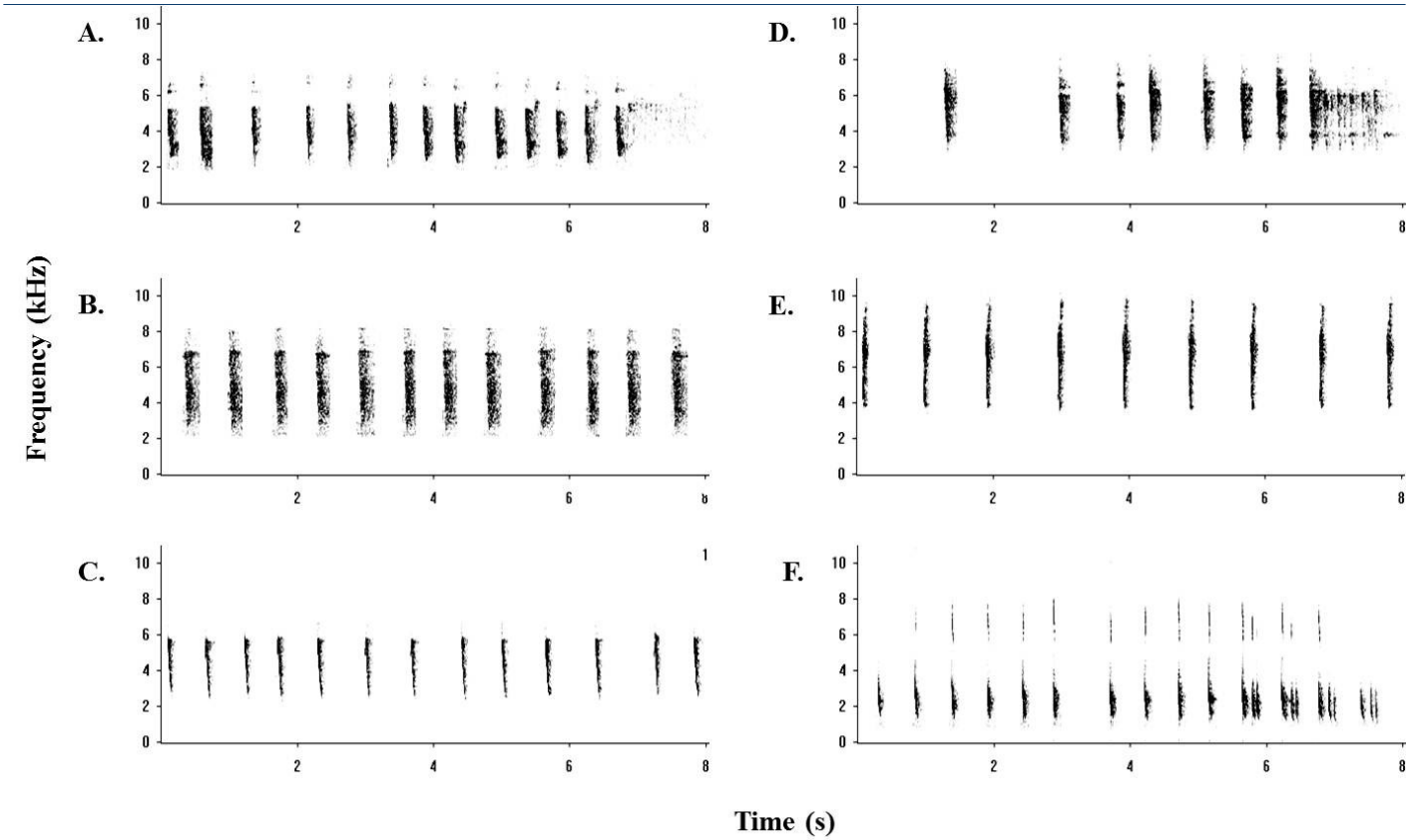

Figure 4. Dawn songs of six subspecies of *Chlorospingus flavopectus* found in Colombia, Venzuela and Bolivia. (A) *C. f. olsoni* (Xeno-canto 12779, O. Laverde), Reserva El Secreto, Garagoa, dpto. Boyacá, Colombia; (B) *C. o. nigriceps* (BSA 16656, D. Calderon-F.), Reserva Los Yalcones, San Agustín, Huila, Colombia; (C) *C. f. eminens* (Xeno-canto 23327, A. Renaudier), Betania, Páramo de Tamá, Táchira, Venezuela: (D) *C. f. fulvigularis* (Xeno-canto 3707, S. Herzog), Old road Cochabamba, Villa Tunari, Carrasco NP, dpto. Cochabamba, Bolivia; (E) *C. f. jacqueti* (BSA 17305, O. Laverde), Agua de la Virgen, Ocaña, dpto. Norte de Santander, Colombia; and (F) *C. f. flavopectus* (BSA 17981, O. Laverde), Finca San Cayetano, vereda Fute, Bojacá, dpto. Cundinamarca, Colombia. Note the final and high-pitched trill in *C. f. olsoni* and *C. f. fulvigularis*, which is not present in other subspecies. In general, *C. f. olsoni* and other Colombian subspecies sing at higher frequency than *C. f. flavopectus*, which has a more complex final trill than *C. f. olsoni* and *C. f. fulvigularis*. Spectrograms were made in Syrinx v2.6h (Burt 2006) applying the same parameters except for adjusting brightness to improve note resolution.

(Buermann *et al.* 2008). Locality records from related Colombian subspecies were gathered from museum specimens, sound recordings, and reliable field observations (Appendix 3). We did not include in the model data of subspecies *flavopectus*, *trudis*, *macarenae* and *phaeocephalus* because they are phylogenetically, vocally and morphologically distinct from other Colombian subspecies, and potentially represent a different species (J. E. Avendaño *et al.*, unpublished data).

Our niche model suggests that *C. f. olsoni* is likely restricted to the middle section of the eastern slope of the Eastern Andes (Fig. 5), apparently tracking the distribution of cloud forest. To the north, *C. f. olsoni* is likely isolated from *C. f. eminens* of the Tamá region by a gap in the foothills of the Sierra Nevada del Cocuy, whereas to the south, the depression of the cordillera at the Las Cruces (Andalucía) Pass in Huila (c. 1200 m) could prevent contact between *C. f. olsoni* and *C. f. nigriceps*, which has been recorded south of Las Cruces at Los Picachos National Park.

Habitat and Ecology.–The new subspecies occurs along a narrow elevational band of cloud forest, between ca. 2,000 and 2,600 m, in the middle section of the eastern slope of the Eastern Andes.

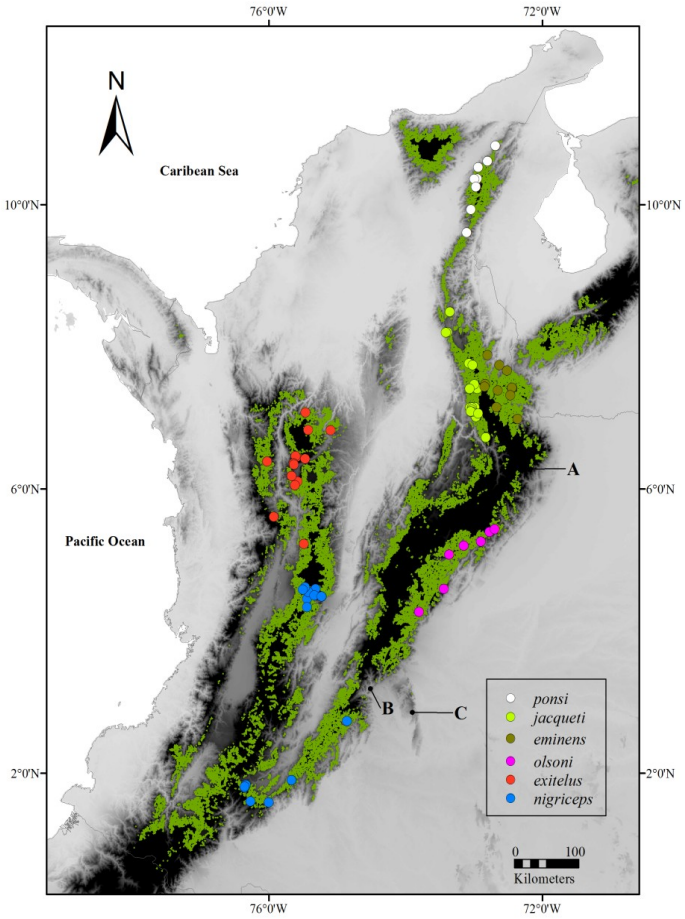

Figure 5. Potential distribution (in green, defined as ≥0.5 presence probability calculated in MAXENT) for six subspecies of *C. flavopectus* in Colombia. Note the restricted potential range of *C. f. olsoni* to the east slope of the Eastern Cordillera between the Sierra Nevada del Cocuy (A) and Las Cruces Pass (B). Locality records are depicted by circles. Subspecies *flavopectus* and *trudis* from the west slope of the Eastern Cordillera, *macarenae* from the Serranía de la Macarena (C) and *phaeocephalus* from the Colombian massif (ranges not shown, see Fig. 1) were not included in the model because they could represent a different species (see text).

Cloud forests in this sector are characterized by high rainfall, relative humidity and cloud cover, with a high abundance and diversity of bryophytes and vascular epiphytes (Bohórquez 2002). The understory is dense, the canopy (20-30 m tall) is broken and irregular due to natural tree-falls over steep slopes and occasional timber extraction (Stiles 1992). At Cerro Comijoque, the Gazaunta drainage and Monterredondo-El Calvario road, forest clearance has been extensive, mainly below *ca.* 2,000 m (Salaman *et al.* 2002). However, *C. f. olsoni* is common in pairs or small conspecific flocks along forest borders and in tall bushes, sometimes in proximity to pastures, much like the other members of the *flavopectus-ophthalmicus* complex.

Nesting.–A nest of *C. f. olsoni* (ICN 110) was collected by C. I. Bohórquez on 7 April 1997 near the Cusiana River, Cerro Comijoque, municipality of Pajarito, Boyacá. It was placed 1 m high and was embedded within mossy vegetation close to the river. The nest was cup-shaped and consisted mainly of moss, fern scales and dead leaves. Its dimensions were: external diameter 133.9 x 101.0 mm, internal diameter 68.6 x 52.0 mm, and depth 35.0 mm. An adult was attending the nest, which contained three eggs (ICN 075). Two of them had small rusty red speckles mainly concentrated near the large end, and measured 19.9 x 15.4 mm and 20.7 x 14.9, respectively. The third egg (20.3 x 15.0 mm) had more speckling along the middle part and the small end. Each egg weighed 2.4 g. This information, combined with gonad sizes from specimens, suggests that *C. f. olsoni* breeds during the middle part of the first semester of year, coinciding with the beginning of the rainiest season for this sector of the Cordillera (Bohórquez 2002). During a bird inventory at Cerro Comijoque in June 1997, most captured species were molting or not breeding (Bohórquez 2002). Clutch size and mass and length of eggs in *C. f. olsoni* are similar to those reported for other related subspecies (Cadena *et al.* 2007).

Conservation.–*C. f. olsoni* has a small range and its habitat is decreasing in extent, with extensive habitat loss below 2,000 m. However, at most localities where it has been recorded, the species occupies secondary forests and tall bushes among mixed forest patches and pastures (as do other members of the *C. flavopectus-ophthalmicus* complex), which implies that as long as some tree

cover is maintained, *C. f. olsoni* will likely resist local extinction.

Discussion

With respect to other members of the *C. flavopectus-ophthalmicus* complex, *C. f. olsoni* is apparently an allopatric taxon diagnosable by traits in plumage, iris coloration and morphometrics. Therefore, it is a valid subspecies under Biological Species Concept; namely, it comprises a distinct population, or group of populations, that occupies a different breeding range from other populations of the same species and individuals are distinguishable from those other populations by one or more phenotypic traits (Remsen 2010).

The phenotypic similarity of *C. f. olsoni*, *exitelus* and *nigriceps* is noteworthy. These taxa are the only northern Andean subspecies with dark heads (*i.e.* brown-black or dark gray), yellow irides and lacking the white postocular spot, which suggests that these character states are derived and homologous. The first two taxa are most similar in crown color and are separated geographically by the very distinct *C. f. nigriceps*, suggesting a leapfrog pattern of geographic variation (Remsen 1984). Their similarity suggests that these three taxa are closely related, and that their common ancestor might have been widely distributed in the Central Andes and the eastern slope of the Eastern Andes. The differentiation of *nigriceps* could be explained by stochastic or selection-driven change producing the leapfrog pattern in color plumage (Remsen 1984, Cadena *et al.* 2011). Alternatively, stabilizing selection on size or color may have produced two allopatric populations (*exitelus-olsoni)* that are similar phenotypically (Patten 2010).

A close relationship between *C. f. exitelus* and *nigriceps* is suggested by a zone of intergradation between them around the headwaters of the Medellín River in the department of Antioquia (Olson 1983). However, *nigriceps* and *olsoni* are apparently isolated on the east slope of the Eastern Andes by the low-lying Las Cruces Pass (*ca.* 1200 m), close to an abrupt environmental change in this area (Graham *et al.* 2010). Further north, *C. f. olsoni* is apparently isolated from the Tamá subspecies *eminens* by a gap at the foothills of the Sierra Nevada del Cocuy. Graham *et al.* (2010) did not report any geographic or environmental discontinuity in this area, possibly because most species they analyzed did not show distributional breaks in this region of the Andes.

However, the Tamá-Cocuy region does appear to constitute the northern or southern limit of the distributions of many montane species and subspecies on the east slope of the Eastern Andes (Hilty & Brown 1986, *cf.* Restall *et al.* 2006). The question remains open as to whether the gap in distribution and subspecies replacements of *C. flavopectus* and other montane birds in this region is the result of an ecological or geographic discontinuity, or simply reflects the lack of sampling in this sector of the east slope. Songs do appear distinct in *C. f. olsoni,* but additional work is needed to confirm if the songs of *olsoni*, *exitelus*, and *nigriceps* differ more from those of other subspecies than among themselves.

As current conservation policy mainly focuses on the species level, additional field and systematic work is necessary to determine species limits within the high phenotypic and genetic diversity that characterizes the *C. flavopectus-ophthalmicus* complex. Currently, *C. flavopectus* is not threatened (Birdlife International 2012). However, given its restriction to the cloud forest within a restricted elevational band, several well differentiated and endemic Colombian subspecies including *olsoni* could be threatened by the accelerated loss of Andean forests (Cavelier 1996,

Etter 2000). Without doubt, *C. flavopectus* is just one example of many Colombian bird species currently not considered threatened but that involve several overlooked valid species that could be possibly threatened presently or in the near future. The conservation of *C. f. olsoni* and other endemic subspecies of the east slope of the Eastern Andes could be enhanced through research on and conservation of other threatened cloud-forest species such as the Black-and-chestnut Eagle *(Spizaetus isidori),* Yellow-eared Parrot *(Ognorhynchus icterotis),* Flame-winged Parakeet *(Pyrrhura calliptera)* and Cundinamarca Antpitta *(Grallaria kaestneri).*

Acknowledgments

We thank the curators and staff of the following museums for permission to examine specimens in their care, and for assistance rendered during our visits: P. Sweet (American Museum of Natural History-AMNH), J. J. Calderón and Y. Rocero (Colección Ornitológica Universidad de Nariño-Uninariño-CO), O. Murillo (Colección Ornitológica Universidad del Valle-Univalle-CO), Y. Molina (Colección Zoológica Universidad del Tolima-CZUT-OR), S. Sierra, F. Forero and C. Medina (Instituto Alexander von Humboldt-IAvH), J. P. López (Instituto de Ciencias Naturales-ICN), S. Cardiff and J. V. Remsen (Louisiana State University Museum of Zoology-LSUMZ), S. Madriñán (Museo Andes-O), F. Ayerbe-Quiñones and M. P. Rivas (Museo de Historia Natural Universidad del Cauca-MHNUC), J. G. Moreno Patiño (Museo de Historia Natural Universidad Industrial de Santander-UIS-AV), D. Perico and Hno. J. E. Espitia (Museo Universidad de La Salle-MLS), C. Peraza (Museo Pontificia Universidad Javeriana-MPJ) and J. Dean and S. L. Olson (National Museum of Natural History-NMNH). For assistance in the field and specimen collection, we thank A. M. Cuervo, J. P. Gómez, N. Gutiérrez, J. P. López, M. Lozano, J. M. Miranda, J. M. Ruiz and S. Sierra. We appreciate tape recordings provided by D. Ascanio, P. Boesman, V. Caro (Banco de Sonidos Animales-BSA), D. Calderón-F., T. Donegan, O. Laverde, M. Medler (Macaulay Library of Natural Sounds-LNS) and Xeno-canto. C. I. Bohórquez collected the nest and eggs cited in this paper. We also thank people that assisted with pictures used in this paper: M. Hennen (Field Museum of Natural History-FMNH), E. R. Briceño, C. Flórez (GAICA-Gobernación de Nariño), A. M. Cuervo, N. Espejo, B. Huertas and T. Donegan (YARÉ/EBA Project) and H. Loaiza. S. González helped with ecological niche modeling analyses and map design. J. P. López took the pictures of specimens at MHNUC.

This paper is a side project of JEA's masters thesis supported by the Facultad de Ciencias at Universidad de los Andes, Fondo Colombia Biodiversa of Fundación Alejandro Ángel Escobar, The Robert Giles' Scholarship of Fundación ProAves, The Explorers' Club and Idea Wild. Museum work conducted by JEA in the United States was supported by the short-term visitor program of the Smithsonian Institution. N. Areta, A. M. Cuervo, D. F. Lane and S. L. Olson provided useful comments on the manuscript.

Literature Cited

ARMENTERAS, D., C. CADENA-V, AND R. P. MORENO.2007. Evaluación del estado de los bosques de niebla y de la meta 2010 en Colombia. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, DC., Colombia.

BIRDLIFE INTERNATIONAL. 2012. Species factsheet: *Chlorospingus ophthalmicus*. Downloaded from http://www.birdlife.org on 21/12/2012

BOHÓRQUEZ, C. I. 2002. La avifauna de la vertiente oriental de los Andes de Colombia. Tres evaluaciones en elevación subtropical. Revista de la Academia de Ciencias Exactas, Físicas y Naturales de Colombia 26:419-442.

BUERMANN, W., S. SAATCHI, T. B. SMITH, B. R. ZUTTA, J. A. CHAVES, B. MILÁ, AND C. H. GRAHAM. 2008. Predicting species distributions across the Amazonian and Andean regions using remote sensing data. Journal of

Biogeography 35:1160-1176.

BURT, J. 2006. Syrinx Version 2.6h, Available at http:// www.syrinxpc.com.

CADENA, C. D., S. CÓRDOBA-CÓRDOBA, G. A. LONDOÑO, D. CALDERÓN-F, T. E. MARTIN, AND M. P. BAPTISTE. 2007. Nesting and singing behavior of Common Bush-Tanagers *(Chlorospingus ophthalmicus)* in South America. Ornitología Colombiana 5:54-63.

CADENA, C. D., Z. CHEVIRON, AND W. C. FUNK. 2011. Testing the molecular and evolutionary causes of a "leapfrog" pattern of geographical variation in coloration. Journal of Evolutionary Biology 24:402-414.

CAVELIER, J., AND A. ETTER. 1996. Deforestation of montane forests in Colombia as a result of ilegal plantations of opium *(Papaver somniferum)*. Pages 541-550 *in* Biodiversity and Conservation of Neotropical Montane Forests (S. Churchill, H. Balslev, E. Forero, and J. Luteyn, Eds.). The New York Botanical Garden, New York.

CUERVO, A. M., P. C. PULGARÍN, D. CALDERÓN-F, J. M. OCHOA-QUINTERO, C. A. DELGADO-V, A. PALACIO, J. M. BOTERO, AND W. A. MÚNERA.2008. Avifauna of the northern Cordillera Central of the Andes, Colombia. Ornitología Neotropical 19:495-515.

DONEGAN, T. M., J. E. AVENDAÑO, B. HUERTAS, AND P. FLÓREZ. 2009. Avifauna de San Pedro de los Milagros, Antioquia: una comparación entre colecciones antiguas y evaluaciones rápidas. Boletín Científico del Museo de Historia Natural 13:63-72.

ETTER, A. 1998. Mapa general de ecosistemas de Colombia. in Informe nacional sobre el estado de la biodiversidad-Colombia. Tomo I. Causas de pérdida de la biodiversidad (M. E. Chaves, and N. Arango, Eds.). Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, PNUMA, Ministerio del Medio Ambiente, Bogotá DC., Colombia.

ETTER, A., AND W. VAN WYNGAARDEN. 2000. Patterns of landscape transformation in Colombia, with emphasis in the Andean region. Ambio 29:432-439.

GARCÍA-MORENO, J., A. G. NAVARRO-SIGÜENZA, A. T. PETERSON, AND L. A. SÁNCHEZ-GONZÁLEZ.2004. Genetic variation coincides with geographic structure in the common bush-tanager *(Chlorospingus ophthalmicus)* complex from Mexico. Molecular Phylogenetics and Evolution 33:186-196.

GRAHAM, C. H., N. SILVA, AND J. VELÁZQUEZ-TIBATÁ. 2010. Evaluating the potential causes of range limits of birds of the Colombian Andes. Journal of Biogeography 37:1863-1875.

HIJMANS, R. J., S. E. CAMERON, J. L. PARRA, P. G. JONES, AND A. JARVIS. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25:1965-1978.

HILTY, S. L., AND W. BROWN. 1986. A Guide to the Birds of Colombia. Princeton University Press, Pricenton, NJ, USA.

ISLER, M. L., AND P. R. ISLER. 1999. The tanagers: natural history, distribution, and identification. Smithsonian Institution Press., Washington, D.C., USA.

OLIVARES, A. 1971. Aves de la ladera oriental de los Andes Orientales, Alto río Cusiana, Boyacá, Colombia. Caldasia 11: 203-226.

OLSON, S. L. 1983. Geographic variation in *Chlorospingus ophthalmicus* in Colombia and Venezuela (Aves: Thraupidae). Proceedings of the Biological Society of Washington 96:103-109.

PATTEN, M. A., AND P. UNITT. 2002. Diagnosability versus mean differences of Sage Sparrow subspecies. Auk 119:26–35.

PATTEN, M. A. 2010. Null expectations in subspecies diagnosis. Ornithological Monographs 67:35-41.

PHILLIPS, S. J., R. P. ANDERSON, AND R. E. SCHAPIRE. 2006. Maximum entropy modelling of species geographic distributions. Ecological Modelling 190:231-259.

REMSEN, J. V. 1984. High incidence of 'leap-frog' pattern of geographic variation in Andean birds: implications for the speciation process. Science 224:171-173.

REMSEN, J. V. 2010. Subspecies as a meaningful taxonomic rank in avian classification. Ornithological Monographs 67:62-78.

RESTALL, R., C. RODNER AND M. LENTINO. 2006. Birds of northern South America, vol. 2: an identification guide. Yale University Press, New Haven, CT, USA.

SALAMAN, P. G. W., F. G. STILES, C. I. BOHÓRQUEZ, M. ÁLVAREZ-R, A. M. UMAÑA, T. M. DONEGAN, AND A. M. CUERVO. 2002. New and noteworthy bird records from the East slope of the Andes of Colombia. Caldasia 24:157-189.

SÁNCHEZ-GÓNZALEZ, L., A. G. NAVARRO-SIGÜENZA, A. T. PETERSON, AND J. GARCÍA-MORENO.2007. Taxonomy of *Chlorospingus ophthalmicus* in Mexico and northern Central America. Bulletin of the British Ornithologists' Club 127:34-49.

SMITHE, F. 1975, 1981. Naturalists' color guide. American Museum of Natural History Press, New York, NY, USA.

STILES, F. G. 1992. A new species of Antpitta (Formicariidae: *Grallaria)* from the Eastern Andes of Colombia. Wilson Bulletin 104:389-399.

ZIMMER, J. T. 1947. Studies of Peruvian birds no. 52. The genera *Sericossypha, Chlorospingus, Cnemoscopus, Hemispingus, Conothraupis, Chlorornis, Lamprospiza, Cissopis* and *Schistochlamys*. American Museum Novitates 1367:4-5.

Recibido: 13 de mayo de 2012. *Aceptado:* 05 de junio de 2013.

Appendix 1. Specimens of Colombian *Chlorospingus flavopectus* subspecies included in the morphometric analyses. Most specimens are from Colombia, unless otherwise stated. For museum acronyms, see acknowledgments.

olsoni ♂ (5): ICN 30940, 36936 (Meta), ICN 17426, 17428, 25592 (Boyacá); ***olsoni*** ♀ (3): ICN 17427, IAvH 3778 (Boyacá), ICN 38090 (Casanare).

exitelus ♂ (10): AMNH 824671, IAvH 8368, NMNH 403746, 427444, 427445, 525953, MLS 4833-5 (Antioquia), IAvH 11938 (Caldas); ***exitelus*** ♀ (2): IAvH 8496, NMNH 403748 (Antioquia).

nigriceps ♂ (18) (include intergradates *nigriceps*>*exitelus*): AMNH 134484, 134486, 134487 (Antioquia), AMNH 113120 (Tolima), AMNH 113117 (Quindío), AMNH 117451, 117452, IAvH 13837, ICN 2632, 2633, 27005, MLS 7100 (Huila), IAvH 2479, ICN 29172, 29174, 33446, NMNH 447806, 447807 (Cauca); ***nigriceps*** ♀ (10): AMNH 134490, 134491, 134492, MLS 4832 (Antioquia), NMNH 256415 (Tolima), ICN 2634, MLS 7101 (Huila), NMNH 447805, 469576, 469577 (Cauca).

ponsi ♂ (16): NMNH 310069, 310070, 310078, 375304 (Colombia, La Guajira), NMNH 375293, 375294, 375295, 375297, 375301, 375302, ICN 36744, 36760, 36782, 36802 (Colombia, Cesar), AMNH 55644, 55645 (Venezuela, Zulia); ***ponsi*** ♀ (13) (all from Colombia): NMNH 310074, 310075, 370073, 370076, 370077, 375303, 375305 (La Guajira), ICN 32689, 35640, 36785, 37139, NMNH 375298, 375300 (Cesar).

jacqueti ♂ (13) (include intergradates *jacqueti*>*eminens*): ICN 2635, 37348, NMNH 375307, 375308, 399160, 399161, 399166, 399167, 399168, 399169 (Norte de Santander), ICN 37329, 37332, NMNH 412811 (Santander); ***jacqueti*** ♀ (7): ICN 2636, 37347, NMNH 375306, 399159, 399163, 399164, 399165 (Norte de Santander).

eminens ♂ (14) (includes intergrades *eminens*>*jacqueti*): IAvH 10631, 12106, 12151, 12177, 12181, 12187, 14837, 14871, 14989, NMNH 403743, 403745, MLS 7093-5 (Norte de Santander); ***eminens*** ♀ (5): IAvH 10647, MLS 7092, 7096, NMNH 403744 (Norte de Santander), ICN 36132 (Santander).

flavopectus ♂ (32): ICN 33500, 34813, 35556, 36157, 36158, 36160, 36161, 36163, 36164, 36166, 36899, 36905, 36910, 36919, NMNH 375309, 375310, 375312 (Santander), IAvH 10288, 11665, 12555, 12284, ICN 33873 (Boyacá), IAvH 11680, ICN 3903, 4746, 4750, 4752, 4753, 4832, 5073, 5075, 11049 (Cundinamarca); ***flavopectus*** ♀ (22): ICN 25496, 36162, 36909, NMNH 375311 (Santander), IAvH 2802, 2819, 10289, 10309, 12227, 12553, 12554, 14198, ICN 2637, 2638, 36867, NMNH 375313 (Boyacá), IAvH 14002, ICN 4745, 4748, 4751, 5072, 5074 (Cundinamarca).

trudis ♂ (5): ANDES-O 602, ICN 37552, 37553, 37569, NMNH 582344 (Santander); ***trudis*** ♀ (4): ICN 37567, 37568, 37571, 37574 (Santander).

macarenae ♂ (4): AMNH 343895, 343897, 343898, NMNH 582348 (Meta); ***macarenae*** ♀ (4): AMNH 343899, 343900, 343901, NMNH 582341 (Meta).

phaeocephalus ♂ (11): AMNH 183248, 186421 (Ecuador, Napo), AMNH 168519, 168520 (Ecuador, El Oro), LSUM 97870, 97872, 97873, 97874, 172403, 179150, 179151 (Peru, Cajamarca); ***phaeocephalus*** ♀ (3): LSUM 97871, 172402, 172404 (Peru, Cajamarca).

Appendix 2. Measurements (means, standard deviations, ranges and sample sizes) discriminated by sex of specimens of ten subspecies of Common Bush -Tanager *Chlorospingus flavopectus* found in Colombia. / = no data available. [a]Length of the culmen from the base to the tip of the upper mandible.

Subspecies	Sex	Total Culmen[a]	Tarsus length	Tail length	Wing chord
olsoni	♂	13.68 ± 0.41 (13.0-14.0) (n=5)	20.72 ± 0.50 (20.2-21.3) (n=5)	60.50 ± 1.68 (58.7-62.8) (n=5)	67.80 ± 1.04 (66.5-69.0) (n=5)
	♀	13.87 ± 0.31 (13.6-14.2) (n=3)	20.87 ± 1.17 (19.6-21.9) (n=3)	61.25 ± 0.07 (61.2-61.3) (n=2)	65.30 ± 3.06 (62.0-68.0) (n=3)
exitelus	♂	13.72 ± 0.5 (13.0-14.5) (n=10)	21.16 ± 0.9 (19.4-22.8) (n=10)	62.43 ± 1.7 (60.1-65.0) (n=9)	70.28 ± 2.6 (66.0-74.0) (n=9)
	♀	13.5 (n=1)	20.35 ± 0.1 (20.3-20.4) (n=2)	63.2 (n=1)	68.0 (n=1)
nigriceps	♂	13.76 ± 0.7 (12.5-14.9) (n=16)	21.18 ± 0.8 (20.0-22.7) (n=16)	62.42 ± 3.0 (56.8-68.9) (n=18)	69.81 ± 2.6 (65.0-74.0) (n=18)
	♀	13.70 ± 0.8 (12.7-15.5) (n=9)	20.97 ± 0.8 (19.9-22.4) (n=9)	61.08 ± 1.7 (59.0-64.1) (n=10)	67.10 ± 2.0 (64.5-71.0) (n=10)
ponsi	♂	13.24 ± 0.83 (12.2-15.5) (n=16)	20.97 ± 0.50 (20.1-21.9) (n=16)	59.96 ± 2.21 (55.4-63.3) (n=16)	68.63 ± 2.02 (63.0-71.5) (n=16)
	♀	13.95 ± 0.35 (12.3-15.5) (n=13)	20.54 ± 0.42 (20.0-21.7) (n=13)	56.32 ± 0.14 (53.6-61.8) (n=13)	63.58 ± 0.35 (61.5-67.0) (n=12)
jacqueti	♂	13.40 ± 0.28 (12.8-14.4) (n=11)	20.62 ± 0.07 (19.6-21.0) (n=11)	59.78 ± 1.84 (56.0-59.5) (n=10)	68.27 ± 0.35 (64.0-71.0) (n=12)
	♀	13.33 ± 0.56 (12.5-14.1) (n=7)	20.35 ± 0.64 (19.6-21.2) (n=7)	57.20 ± 1.01 (53.0-58.2) (n=5)	63.83 ± 0.93 (61.0-65.0) (n=7)
eminens	♂	13.21 ± 0.49 (12.4-14.0) n=14	20.85 ± 1.08 (19.7-24.1) n=14	62.80 ± 2.56 (59.0-69.9) n=13	69.93 ± 1.43 (67.0-72.5) n=14
	♀	12.54 ± 0.61 (11.5-13.0) n=5	20.78 ± 1.17 (19.6-22.5) n=5	56.92 ± 1.97 (54.9-59.8) n=5	65.2 ± 1.52 (63.0-67.0) n=5
flavopectus	♂	14.10 ± 0.62 (12.6-15.1) (n=31)	22.27 ± 0.85 (19.3-24.7) (n=30)	64.24 ± 2.48 (60.2-70.5) (n=30)	71.80 ± 2.62 (62.5-78.0) (n=32)
	♀	14.18 ± 0.69 (13.0-15.7) (n=22)	22.13 ± 0.89 (20.5-23.6) (n=22)	61.40 ± 2.42 (55.4-67.9) (n=21)	67.91 ± 2.57 (64.0-76.0) (n=22)
trudis	♂	13.92 ± 0.70 (13.0-14.8) (n=5)	22.70 ± 0.57 (22.0-23.3) (n=5)	63.28 ± 2.59 (60.7-67.1) (n=5)	69.40 ± 2.82 (66.0-73.0) (n=5)
	♀	14.28 ± 0.63 (13.4-14.9) (n=4)	22.60 ± 1.15 (21.1-23.9) (n=4)	62.80 ± 5.83 (58.9-69.5) (n=3)	65.25 ± 0.65 (64.5-66.0) (n=4)
macarenae	♂	12.95 ± 0.87 (11.7-13.7) (n=4)	21.25 ± 1.35 (19.7-22.7) (n=4)	60.65 ± 1.39 (59.3-62.4) (n=4)	67.00 ± 1.91 (64.5-68.5) (n=4)
	♀	13.15 ± 0.33 (12.8-13.6) (n=4)	20.75 ± 0.79 (19.6-21.4) (n=4)	55.53 ± 0.46 (55.0-55.8) (n=3)	61.75 ± 0.65 (61.0-62.5) (n=4)
phaeocephalus	♂	14.05 ± 0.32 (12.8-14.6) (n=10)	21.69 ± 1.05 (18.9-23.3) (n=11)	59.83 ± 2.82 (47.9-64.6) (n=11)	69.59 ± 4.19 (59.0-73.0) (n=11)
	♀	13.73 ± 0.25 (13.5-14.0) (n=3)	21.67 ± 0.50 (21.2-22.2) (n=3)	57.95 ± 0.49 (57.6-58.3) (n=2)	64.50 ± 2.18 (63.5-67.0) (n=3)

Appendix 3. Supporting information of locality data used in ecological niche modeling analysis. For acronyms for museum specimens and sound recordings see acknowledgments.

Subsp.	Source	Locality	Latitude	Longitude
ponsi	NMNH 375293-300	La Guajira, Hiroca	9,9328	-73,0428
ponsi	NMNH 375303-5	La Guajira, La África	10,5239	-72,9354
ponsi	NMNH 370077-8	La Guajira, SE Fonseca, Monte Elías, Tierra Negra	10,8316	-72,6856
ponsi	NMNH 310069-71,73-76	La Guajira, SE Fonseca, Tierra Nueva	10,6144	-72,8011
ponsi	ICN 36744	Cesar, Manaure, Vda. El Cinco, arriba del Cinco	10,3640	-72,9474
ponsi	ICN 37139	Cesar, Manaure, Vda. San Antonio, Finca Villa Luz	10,3636	-72,9930
ponsi	ICN 35640	Cesar, La Paz, Cgto. San José, Vda. Alto de Perijá	10,2500	-72,9667
ponsi	ICN 32698	Cesar, La Jagüa de Ibirico, Vda. El Zumbador	9,6069	-73,1018
jacqueti	NMNH 375306-8	Norte de Santander, Convención	8,4910	-73,3521
jacqueti	ICN 37347-8	Norte de Santander, Ocaña, Vda. Agua de la Virgen	8,2077	-73,3852
jacqueti	ICN 2635-6	Norte de Santander, La Palmita	8,1992	-73,4095
jacqueti	Olson (1983)	Norte de Santander, Ramírez	7,7667	-73,0686
jacqueti	Olson (1983)	Norte de Santander, Las Ventanas	7,7442	-73,0147
jacqueti	ICN 36132	Santander, Suratá, Vda. El Palchal, Sector Pangote	7,4089	-72,9469
jacqueti	Olson (1983)	Santander, Cachirí	7,4722	-72,9927
jacqueti	R. Herrera pers. com.	Matanza, Cgto. Santa Cruz de la Colina, vda. Sinay	7,4095	-73,0614
jacqueti	JEA pers. obs.	Tona, vda. Retiro Grande, Fca. El Brasil	7,1426	-73,0543
jacqueti	JEA pers.obs.	Tona, vda. La Plazuela, Reserva AMB	7,1485	-72,9850
jacqueti	Olson (1983)	Santander, La Corcova	7,1447	-73,0275
jacqueti	JEA pers. obs.	Floridablanca, Cgto. De la Corcova, Reserva Natural El Diviso	7,1122	-73,0300
jacqueti	ICN 37329	Santander, Piedecuesta, Vda. Cristales, Reserva El Rasgón	7,0401	-72,9889
jacqueti	JEA pers. obs.	Santander, Piedecuesta, vda. Planadas	7,0136	-72,9692
jacqueti	JEA pers. obs.	Santander, Piedecuesta, Vda. La Mata alta	7,0845	-73,0266
jacqueti	ICN 37332	Santander, Floridablanca, Vda. La Judía, Reserva Los Maklenkes	7,0901	-73,0458
jacqueti	JEA pers. obs.	Santander, San Andrés, Vda. Santa Cruz, Finca El Tablón	6,7206	-72,8216
jacqueti	Olson (1983)	Santander, Hacienda Las Vegas	7,0616	-72,9353
eminens	IAvH 14837	Norte de Santander, PNN Tamá, Herrán, Centro de visitantes	7,4167	-72,4347
eminens	IAvH 14871	Norte de Santander, PNN Tamá, Herrán, Sendero Arenal	7,4167	-72,4348
eminens	IAvH 14989	Norte de Santander, PNN Tamá, Herrán, entrada del Parque	7,4167	-72,4347
eminens	IAvH 10631, 47	Norte de Santander, Herrán, PNN Tamá, sector Orocué	7,4253	-72,4439
eminens	IAvH 12151	Norte de Santander, Cucutilla, vereda Carrizal, queb. Poveda	7,4769	-72,8318
eminens	IAvH 12106	Norte de Santander, Cucutilla, vereda Carrizal, queb. Grande	7,4389	-72,8408
eminens	Olson (1983)	Norte de Santander, Palo gordo, 10 miles S.E. Villa Felisa	7,6667	-72,5167
eminens	Olson (1983)	Norte de Santander, Gramalote	7,8833	-72,8000
eminens	ICN 18195	Norte de Santander, Toledo	7,3167	-72,4667
eminens	NMNH 403743-45	Norte de Santander, Cúcuta, Villa Felisa	7,7402	-72,6265
eminens	MLS 7094-6	Norte de Santander, Chitagá	7,1500	-72,6667
eminens	MLS 7092-3	Norte de Santander, Pamplona	7,3833	-72,6500
eminens	Olson (1983)	Boyacá, Cubará, Hacienda La Primavera	6,9829	-72,3597
olsoni	ICN 17426-8, 25592	Boyacá, Pajarito, falda W Cerro de Comijoque	5,3919	-72,7703
olsoni	Bohórquez (2000)	Boyacá, Pajarito, Cerro Comijoque	5,4347	-72,6917

Subsp.	Source	Locality	Latitude	Longitude
olsoni	Foto (N. Espejo)	Boyacá, Miraflores, Cerro La Rusa	5,1981	-73,1481
olsoni	Xenocanto 12778-9	Boyacá, Garagoa, Vereda Ciénaga-Valvanerra, Reserva el Secreto	5,0744	-73,3611
olsoni	ICN 38090	Casanare, Chámeza, vereda Centro norte	5,2569	-72,8979
olsoni	ICN 30940	Cundinamarca, Guayabetal, vía Monterredondo-El Calvario	4,2674	-73,8001
olsoni	O. Cortes pers.com.	Cundinamarca, Medina, vda. Miralindo, ca. río Gazaunta	4,5928	-73,4395
nigriceps	Bohórquez (2000)	Caquetá, San Vicente del Caguán, Snia de los Picachos	2,7303	-74,8553
nigriceps	ICN 33446	Cauca, Santa Rosa, Vda. Petrólea, Playón: Snía. de los Churumbelos	1,6000	-76,2667
nigriceps	NMNH 117452	Huila, Andalucía	1,9000	-75,6667
nigriceps	CZUT-OR 77	Tolima, Cajamarca, vda. Cristales, Río Bermellón	4,4514	-75,4383
nigriceps	CZUT-OR 81, 249	Tolima, Ibagué, Juntas, Queb. Las Perlas	4,5894	-75,3147
nigriceps	CZUT-OR 289	Tolima, Ibagué, Danta/Las Pavas	4,3353	-75,4369
nigriceps	ANDES-O 571	Tolima, Ibagué, Clarita Botero	4,4840	-75,2244
nigriceps	NMNH 256415	Tolima, Ibagué, Río Toche	4,5500	-75,4167
nigriceps	AMNH 113117	Tolima, El Edén	4,5000	-75,3333
nigriceps	ICN 31462	Quindío, Salento, La Picota, PRN Alto Quindío, queb. Cárdenas	4,6167	-75,4667
nigriceps	Olson (1983)	Quindío, Laguneta	4,5833	-75,5000
nigriceps	AMNH 117451	Huila, La Candela	1,8333	-76,3333
nigriceps	ICN 27005	Huila, Acevedo, PNN Cueva de los Guácharos, ca. Guácharos cave	1,5833	-76,0000
nigriceps	IAvH 13837	Huila, San Agustín, La Castellana, campamento el Palmar	1,7956	-76,3514
nigriceps	BSA 16657	Huila, San Agustín, La Castellana, Reserva Natural los Yalcones	1,8100	-76,3497
exitelus	Cuervo et al. (2008)	Antioquia, Amalfi, Cajamarca, Fca. Canales	6,8235	-75,0935
exitelus	Donegan et al. (2009)	Antioquia, San Pedro de los Milagros, Vda. La Lana, Fca. José León	6,4494	-75,5942
exitelus	Donegan et al. (2009)	Antioquia, San Pedro de los Milagros, vda. La Lana Fca. Lasallista	6,4636	-75,6069
exitelus	Donegan et al. (2009)	Antioquia, San Pedro de los Milagros, vda. Ovejas	6,3585	-75,6357
exitelus	Donegan et al. (2009)	Antioquia, San Pedro de los Milagros, vda. El Apretel	6,4236	-75,4677
exitelus	IAvH 8368	Antioquia, Envigado, Alto San Sebastián de la Castellana	6,1026	-75,5804
exitelus	A. M. Cuervo pers.obs.	Antioquia, Medellín, Cgto. San Antonio de Prado, Alto El Silencio	6,1833	-75,6667
exitelus	NMNH 403746	Antioquia, Valdivia, Ventanas	7,0744	-75,4602
exitelus	NMNH 427444-5	Antioquia, Hda. Zulaiba, 17 miles NE Santa Rosa de Osos	6,8310	-75,4243
exitelus	AMNH 824670	Antioquia, Caldas, El Cardal	6,0489	-75,6190
exitelus	IAvH 11983	Caldas, Aranzazu, Vda. El Laurel, Hda. Termopilas	5,2254	-75,4847
exitelus	D. Calderon-F pers.com.	Antioquia, Caicedo, La Noque	6,3833	-73,0167
exitelus	D. Calderon-F pers. com.	Antioquia, Andes, vda. Santa Rita, Fca. La Reina	5,5882	-75,9294
exitelus	D. Calderon-F pers. com.	Antioquia, Bello, Las Baldías	6,3439	-75,6244