



UNIVERSITY OF CALIFORNIA PRESS
JOURNALS + DIGITAL PUBLISHING



The American
Ornithologists' Union

A NEW SPECIES OF BARBET (CAPITONIDAE: CAPITO) FROM THE CERROS DEL SIRA, UCAYALI, PERU

Author(s): Glenn Fairbanks Seeholzer, Bachelor of Science, Benjamin M Winger, Michael G. Harvey, Daniel Cáceres A. and Jason D Weckstein

Reviewed work(s):

Source: *The Auk*, (-Not available-)

Published by: [University of California Press](#) on behalf of the [American Ornithologists' Union](#)

Stable URL: <http://www.jstor.org/stable/10.1525/auk.2012.11250>

Accessed: 12/07/2012 13:15

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



University of California Press and American Ornithologists' Union are collaborating with JSTOR to digitize, preserve and extend access to *The Auk*.

<http://www.jstor.org>



**A NEW SPECIES OF BARBET (CAPITONIDAE: CAPITO) FROM
THE CERROS DEL SIRA, UCAYALI, PERU**

Journal:	<i>The Auk</i>
Manuscript ID:	AUK-11-250.R1
Manuscript Type:	Research Article
Date Submitted by the Author:	08-Mar-2012
Complete List of Authors:	Seeholzer, Glenn; Cornell Lab of Ornithology, ; Louisiana State University, Museum of Natural Science Winger, Benjamin; The University of Chicago, Committee on Evolutionary Biology Harvey, Michael; Cornell Lab of Ornithology, ; Louisiana State University, Museum of Natural Science Cáceres A., Daniel; Universidad de San Agustín, Museo de Historia Natural Weckstein, Jason; The Field Museum, Zoology-Bird Division
Keywords:	Peru, outlying ridges, Capito, Cerros del Sira, new species

SCHOLARONE™
Manuscripts



The Auk 129(3):1–9, 2012
 © The American Ornithologists' Union, 2012.
 Printed in USA.

A NEW SPECIES OF BARBET (CAPITONIDAE: *CAPITO*) FROM THE CERROS DEL SIRA, UCAYALI, PERU

GLENN F. SEEHOLZER,^{1,2,6} BENJAMIN M. WINGER,^{1,3,4} MICHAEL G. HARVEY,^{1,2} DANIEL CÁCERES A.,⁵ AND JASON D. WECKSTEIN⁴

¹Cornell Lab of Ornithology, 159 Sapsucker Woods Road, Ithaca, New York 14850, USA;

²Museum of Natural Science, 119 Foster Hall, Louisiana State University, Baton Rouge, Louisiana 70803, USA;

³Committee on Evolutionary Biology, University of Chicago, 1025 E. 57th Street, Culver Hall 402, Chicago, Illinois 60637, USA;

⁴Department of Zoology, Field Museum of Natural History, 1400 S. Lake Shore Drive, Chicago, Illinois 60605, USA; and

⁵Museo de Historia Natural, Universidad Nacional de San Agustín, Avenida Daniel Alcides Carrión s/n, Arequipa, Perú

ABSTRACT.—We describe a new species of barbet in the genus *Capito* from an outlying ridge of the eastern Andes of Peru. We performed phylogenetic and population genetic analyses of mitochondrial DNA sequences of the new species and *C. wallacei* and determined that they are reciprocally monophyletic sister species. The new species is diagnosable by plumage and morphology from *C. wallacei* and is apparently endemic to a small region of montane cloud forest in the southern portion of the Cerros del Sira. Received 3 November 2011, accepted 27 March 2012.

Key words: *Capito*, Cerros del Sira, new species, outlying ridges, Peru.

Una Nueva Especie de Capitonidae (*Capito*) de los Cerros del Sira, Ucayali, Perú

RESUMEN.—Describimos una nueva especie de género *Capito* de un ramal montañoso de los Andes orientales del Perú. Realizamos un análisis filogenético y de genética de poblaciones con base en secuencias de ADN mitocondrial y determinamos que la nueva especie y *C. wallacei* son especies hermanas y recíprocamente monofiléticas. La nueva especie es diagnosticable por plumaje y morfología de su especie hermana, *C. wallacei*, y aparentemente es endémica de una región restringida de bosque nublado en el sector sur de los cerros del Sira.

THE DISCOVERY OF bird species new to science in the past four decades has served as a reminder of the remarkable degree of undescribed avian species diversity that still exists (e.g., Krabbe et al. 1999, O'Neill et al. 2000, Lane et al. 2007). Although new avian species have been described from across the globe, no region rivals the Andes of South America in the rate of new species discovery. Many newly described bird species are restricted to small geographic ranges, and the logistical challenges associated with travel in these regions have often prevented earlier exploration. The Cerros del Sira (hereafter "Sira"), in the departments of Ucayali, Junín, and Pasco, Peru, is one isolated region that has received few visits by ornithologists. From 4 September to 16 November 2008, a team composed of D.C.A., M.G.H., G.F.S., and B.M.W. conducted the first intensive ornithological inventory of the southern portion of the Sira (Harvey et al. 2011). Previous ornithological work in the Sira had been restricted to the northern portion of the range, which is isolated from the highlands of the southern part of the Sira by a low-elevation saddle (Weske and Terborgh 1971, 1977; Terborgh and Weske 1975; Graves and Weske 1987; Mee et al. 2002; Gastañaga et al. 2007). On 8 October 2008, while the field team was scouting for new camp locations on the eastern slope of

the Sira in the Río Tzipani valley, M.G.H. encountered a barbet of the genus *Capito* with unique plumage characters in a mixed-species flock at 1,225 m. The barbet resembled the Scarlet-banded Barbet (*Capito wallacei*), which had never been seen away from its type locality in the Cordillera Azul, 440 km to the north. This individual, a female, was collected by E. Camayteri and prepared as a study skin, with tissue preserved in ethanol.

Because of logistical difficulties, further work at this locality was not feasible. Instead, the team established a camp at 1,000 m on the northern ridge of the upper Río Shinipo watershed, hoping to find the barbet in a different location. This new locality was 18.5 km north of the Río Tzipani locality where the first specimen had been collected, but the sites shared similar topography, elevation, and habitat. On 31 October 2008, the field team found the new barbet at the upper Río Shinipo locality and spent the subsequent 6 days making ecological and behavioral observations. Seven additional specimens were collected and prepared as study skins with tissue samples preserved in ethanol. The specimens were subsequently compared with the type series of *C. wallacei* and were determined to represent a distinct species that we are honored to name:

⁶E-mail: seeholzer.glenn@gmail.com

***Capito fitzpatricki*, sp. nov.**

Sira Barbet

Barbudo del Sira (Spanish)

Holotype.—Centro de Ornitología y Biodiversidad (CORBIDI) no. 2793, adult female, 11.45 km west-southwest of the mouth of Quebrada Shinipo, Cerros del Sira, Región Ucayali, Peru (10°31'48"S, 74°07'12"W); elevation 1,050 m; collected 1 November 2008 by G.F.S.; study skin and tissue prepared by G.F.S.; audio-recorded by G.F.S. (Macaulay Library of Natural Sounds, Cornell Laboratory of Ornithology, Ithaca, New York; ML AUDIO 138799).

Diagnosis.—The new form is assignable to the genus *Capito* on the basis of strong similarity to the plumage and morphology of *C. wallacei*, as well as to all other *Capito* taxa (for generic diagnosis, see O'Neill et al. 2000). In all plumages, *C. fitzpatricki* differs from *C. wallacei* by (1) flank coloration, (2) breast-band width and coloration, (3) lower back coloration, and (4) thigh feather coloration (Fig. 1). *Capito fitzpatricki* has broad Oxblood Red flanks (capitalized color names follow Ridgway 1912), whereas *C. wallacei* exhibits flanks sparsely washed with yellow-orange. The Nopal Red breast-band of *C. fitzpatricki* averages 22.8 mm at center, whereas the Scarlet-Red breast-band of *C. wallacei* averages 15.6 mm at center (Table 1). In *C. fitzpatricki*, a white line extends mid-dorsally from the red of the lower back to the uppertail coverts. In our examination, this region in *C. wallacei* was tinged pale yellow, although O'Neill et al. (2000) described it as "white" in their examination of the same specimens. Finally, *C. fitzpatricki* has black outer thigh feathers sparsely tipped with yellow, whereas *C. wallacei* exhibits gray outer thigh feathers more extensively tipped with yellow. The females of *C. fitzpatricki* are additionally distinguished from *C. wallacei* by the presence in *C. fitzpatricki* of Scarlet outermost scapular feathers tipped with Pale Lemon Yellow (as opposed to Picric Yellow) and the absence in *C. fitzpatricki* of two characters: white-tipped sub-ocular feathers (but see below for exception) and buffy-white spots on the secondaries. Additionally, measurements of wing, tail, and bill depth are larger, on average, in *C. fitzpatricki* than in *C. wallacei* (Table 1).

Description of holotype.—Forehead, crown, nape Oxblood Red merging into an Oxblood Red upper mantle. Supercilium white, beginning at front of eye and extending posteriorly without broadening to just past the posterior edge of the ear coverts. Three black rictal bristles (longest 12 mm) extending from the feather margin of both nares. Lores, narrow strip above eye, 5-mm-long strip below eye and ear coverts black, forming a mask, which merges into black scapulars. Single black subocular feather under left eye tipped white. Throat and upper breast white, bordered below by 24.4-mm-wide Nopal Red breast-band. The red breast-band is continuous with broad Oxblood Red flanks sparsely tipped with Picric Yellow. Gray bases of flank feathers are more apparent closer to axillaries. Small area of center of belly just below breast-band Picric Yellow fading into Sea-foam Yellow on the lower belly and undertail coverts. Outer tibial feathers black with diffuse Picric Yellow, inner tibial feathers white and Sea-foam Yellow. Back black with narrow posteriorly tapered mantle of Oxblood Red feathers, a continuation of the red nape feathering, the lower mantle feathers with 3.3-mm yellow tips fading from Picric Yellow to Martius Yellow. Scapulars black with outermost rows of feathers variably Scarlet interspersed with Pale Lemon Yellow. Red and yellow scapular feathering meets the red mantle feathering on back. At the lateral and posterior border of the red mantle, a strip of white feathers extends posteriorly, tapering at the upper tail coverts; otherwise, lower back is black. Wings dark, all primaries dark brown (from wear) contrasting slightly with blacker, presumably fresher secondaries. Edging of outer webs of primaries dull olive-green and worn. All remiges, except P10, with broad yellowish-white on inner vane. Underwing coverts pale yellow with white feathers at base of primaries. Rectrices black.

Soft parts recorded at time of collection: irides dark red; maxilla bluish gray with distal half and tomium darker bluish gray (approaching black) than proximal half; mandible bluish gray with distal half and tomium darker bluish gray (approaching black) than proximal half; feet and tarsi blue-gray; toe pads orange.

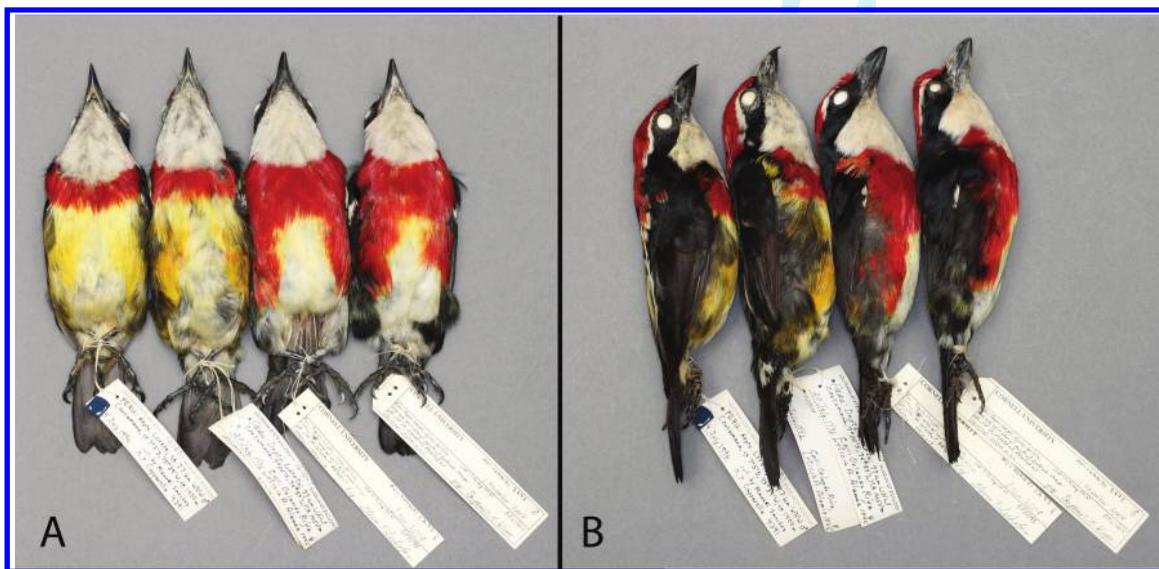


FIG. 1 (A) Ventral and (B) lateral view of (from left to right) *Capito wallacei* (male, LSUMZ 161647), holotype of *C. wallacei* (female, MUSM 21269), holotype of *C. fitzpatricki* (female, AU-CORBIDI 2793), and *C. fitzpatricki* (male, AU-CORBIDI 2192).

TABLE 1. Summary of mass (g) taken from specimen field tags and morphological and plumage measurements (mm) from the specimens of *Capito fitzpatricki* and *C. wallacei* used in morphometric analyses (see text). For each variable, the first line is the population mean (\pm SD) with sample size in parentheses, and the second line is the maximum and minimum value. Significant differences from a two-tailed *t*-test between species are indicated by asterisks (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$); *C. fitzpatricki* is larger in all significant comparisons.

	Species	
	<i>C. fitzpatricki</i>	<i>C. wallacei</i>
Mass (g)*	73.9 \pm 3.4 (9) 79, 70	69.5 \pm 5.3 (13) 78, 63
Culmen (mm)	16.13 \pm 0.82 (8) 17.26, 14.73	15.95 \pm 0.58 (11) 16.69, 14.89
Wing (mm)**	94.5 \pm 2.3 (9) 97.6, 90.4	91.0 \pm 2.02 (11) 95.4, 88.0
Tail (mm)	56.3 \pm 2.2 (9) 60, 53	55.6 \pm 1.7 (10) 58, 53
Tarsus (mm)*	25.02 \pm 0.90 (9) 26.18, 24.16	23.60 \pm 1.48 (10) 25.63, 20.79
Bill depth (mm)***	11.03 \pm 0.49 (9) 11.97, 10.58	9.42 \pm 0.37 (11) 10.05, 8.87
Breast-band width (mm)***	22.76 \pm 2.13 (9) 25.75, 19.33	15.59 \pm 2.17 (5) 18.57, 12.61

Measurements of holotype.—Culmen (nares to tip) 15.13 mm, wing length (flattened) 93.32 mm, tail 54 mm, tarsus 24.17 mm, bill depth at anterior end of nares 10.58 mm, ovary damaged in collection, largest intact follicle 3 \times 3 mm, skull 100% ossified, no bursa, body mass 78.0 g.

Specimens examined.—*Capito fitzpatricki*: Type series of eight (holotype and seven paratypes; four males, four females), all prepared as conventional study skins. Seven are from the type locality: Cornell University Museum of Vertebrates (CUMV) 53126; University of Kansas Natural History Museum (KUNHM) 117325 and 117326; and Centro de Ornitología y Biodiversidad (AU-CORBIDI) 2792, 2793, 2795, 2796. CUMV 53125 is from the Río Tzipani locality (see below; Table 2 and Fig. 2). Two additional specimens of *C. fitzpatricki* were collected on 20 July 2011 at Quebrada Quirapokiarí (see below): CORBIDI field catalog no. SFR 739 and LSUMZ field catalog no. GFS 653. These were not available for direct comparison

with the type series; thus, we do not consider them paratypes here. However, these two specimens exhibit the same plumage features as the type series and were incorporated in the morphometric analyses below. *Capito wallacei*: Eleven from the type series of *C. wallacei* (5 males, 6 females) from 77 km WNW Contamana, Loreto, Peru (07°05'S, 75°39'W): Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (MUSM) no. 21269 (*C. wallacei* holotype), 17570, 17571, 17572, 17573, and 17574 and Louisiana State University Museum of Natural Science (LSUMZ) 161645, 161646, 161650, 161651. Ten are study skins; LSUMZ 161648 is a partial study skin and partial skeleton.

Distribution.—Known from three localities on the east slope of the southern Cerros del Sira, Ucayali, Peru (Fig. 3): (1) north ridge of upper Río Tzipani watershed (10°41'24"S, 74°05'56"W), 1,250 m; (2) north ridge of upper Río Shinipo watershed (10°31'48"S, 74°07'12"W), 950–1,100 m (type locality); and (3) north ridge of Quebrada Quirapokiarí watershed, 22.86 km southwest mouth of Río Cohengua (10°25'12"S, 74°9'0"W), 1,150–1,250 m.

Etymology.—It is our pleasure to name this species in honor of John W. Fitzpatrick. During his career as a graduate student at Princeton University, curator of birds and chair of zoology at the Field Museum of Natural History, director of the Archbold Biological Station, and director of the Cornell Lab of Ornithology, Dr. Fitzpatrick has had an immeasurable influence on ornithology and bird conservation and has inspired generations of young ornithologists, including M.G.H., G.F.S., and B.M.W. during their undergraduate years at Cornell. In particular, we honor his remarkable contributions to knowledge of Peruvian birds, as exemplified by a series of expeditions that he led to Peru between 1974 and 1985 that resulted in the description of six bird species new to science (Fitzpatrick et al. 1977, 1979; Fitzpatrick and O'Neill 1979, 1986; Fitzpatrick and Willard 1990; Fitzpatrick and Stotz 1997). The English and Spanish names recognize the isolated mountain range to which this species is apparently restricted.

REMARKS

Variation in the type series.—In Figure 2, we present the type series of eight specimens that were collected and prepared in 2008. Within the series of adult specimens, males differ from females in lacking red and yellow pigmentation on the scapulars and exhibiting darker, more saturated red feathering on the crown and flanks. Males are also smaller than females, on average, although

TABLE 2. Museum numbers, localities, sexes, and morphological measurements of the *Capito fitzpatricki* type series. Localities are indicated as (A) north ridge of upper Río Tzipani watershed (10°41'24"S, 74°05'56"W), 1,250 m; or (B) north ridge of upper Río Shinipo watershed (10°31'48"S, 74°07'12"W), 950–1,100 m (type locality).

Museum number	Locality	Elevation (m)	Sex	Mass (g)	Culmen (mm)	Wing (mm)	Tail (mm)	Tarsus (mm)	Bill depth (mm)
AU-CORBIDI 2793 ^a	B	1,050	F	78	15.13	93.32	54	24.17	10.58
CU 53125	A	1,267	F	73	17.26	97.62	53	24.16	10.76
CU 53126	B	1,050	F	70	16.38	96.86	58	24.24	10.74
KUNMH 117326	B	1,050	F	73	14.73	93.58	56	25.79	10.70
AU-CORBIDI 2792	B	1,050	M	70	—	94.13	58	26.18	10.61
AU-CORBIDI 2795	B	1,050	M	72	15.46	94.89	56	—	9.27
AU-CORBIDI 2796	B	1,050	M	73	16.2	94.24	57	24.16	11.97
KUNMH 117325	B	1,050	M	72	16.45	90.38	55	24.70	11.33

^aHolotype.



FIG. 2. Lateral views of the type series of *Capito fitzpatricki*: (from right to left) CU 53125 (female), CU 53126 (female), AU-CORBIDI 2793 (female; holotype), KUNMH 117326 (female), KUNMH 117325 (male), AU-CORBIDI 2792 (male), AU-CORBIDI 2796 (male), and AU-CORBIDI 2795 (subadult male). The subadult male shows paler red flanks compared to the rest of the series and had incomplete skull ossification.

this difference was not significant ($F = 0.114$, $df = 1$, $P = 0.740$). Of the four males, one is presumed to be a subadult because of its limited skull ossification (20%) and paler, less saturated red flanks and crown. The three adult males exhibit variation in the length of the yellow tips on the lower mantle feathers; the yellow tips of these feathers on KUNMH 117325 and AU-CORBIDI 2796 are approximately one-third of the length of those found on the holotype. This variation in the length of the yellow tips on the lower mantle feathers is also observed in the females of the type series; CUMV 53126 exhibits yellow tips of 1 mm or less, whereas all other females have yellow tips of 2–3 mm. CUMV 53126 also has the palest shade of red on the crown of any specimen in both sexes (nearest Spectrum Red). Unlike all other *C. fitzpatricki* specimens, AU-CORBIDI 2793 (a female) possesses a single white feather fleck below its left eye. Extensive white feather flecking below the eye is a feature exhibited by all female specimens of *C. wallacei*.

Distribution and habitat.—*Capito fitzpatricki* is presently known from three localities within a 30-km section of the Sira, an outlying ridge of the Andes in central Peru. All localities are on the crests of ridges that descend east into the lowlands from the main spine of the Sira in the Ucayali Department (for further site details, see Harvey et al. 2011). We first encountered the species on the north ridge of the upper Río Tzipani watershed in the highest stratum of tall (30 m) montane forest with a sparse understory of palms and woody vegetation. However, we made the majority of our observations at the type locality, from a trail that traversed the north ridge of the upper Río Shinipo watershed. The highest elevation reached along this trail was 1,250 m, and we made most of our observations between 950 m and 1,100 m.

It seems likely that *C. fitzpatricki* occurs along the length of the east slope of the southern Sira at appropriate elevations and in

suitable habitat. Reports of the presence of this species on the west slope of the southern Sira (10°42'S, 74°11'W) by our local Ashéninka guides have credence because of their apparent familiarity with the species. Although appropriate elevations and potentially suitable habitat exist on the southern Sira's west slope, we only surveyed the area in transit, and more thorough surveys are needed to confirm the presence of *C. fitzpatricki*.

It is unlikely that the range of *C. fitzpatricki* extends to the isolated northern Sira. *Capito fitzpatricki* has not been found during ornithological surveys on the west slope of the northern Sira (Terborgh and Weske 1975, Mee et al. 2002, Gastañaga et al. 2007), including a recent survey (July and August 2010) by colleagues informed of its potential presence (J. Socolar pers. comm.). A team of biologists who visited appropriate elevations on the east slope of the northern Sira in 2010, where they mist netted but did not conduct observational surveys or make audio recordings, did not detect *C. fitzpatricki* (J. Graham pers. comm.).

To the south of the known range of *C. fitzpatricki*, the humid lower montane forests of the southernmost section of the Sira are isolated by the drier subtropical valley of the Río Unine, a tributary of the Ucayali River (Fig. 3). South of the Río Unine, lower montane forest stretches almost continuously west to the main chain of the Andes. M.G.H. did not detect *C. fitzpatricki* in appropriate habitat and elevations south of the Río Unine on Cerro Quitchungari (11°03'S, 74°11'W) on 16–17 November 2008 despite playback of calls known to elicit a response at the type locality (Harvey et al. 2011).

At the type locality, the montane forest along the peaks of the ridge crest was generally lower in stature in relation to the ~30-m-tall forest of the slopes and valleys between ridges (Fig. 4). We observed *C. fitzpatricki* in both types of forest. Arboreal epiphytes

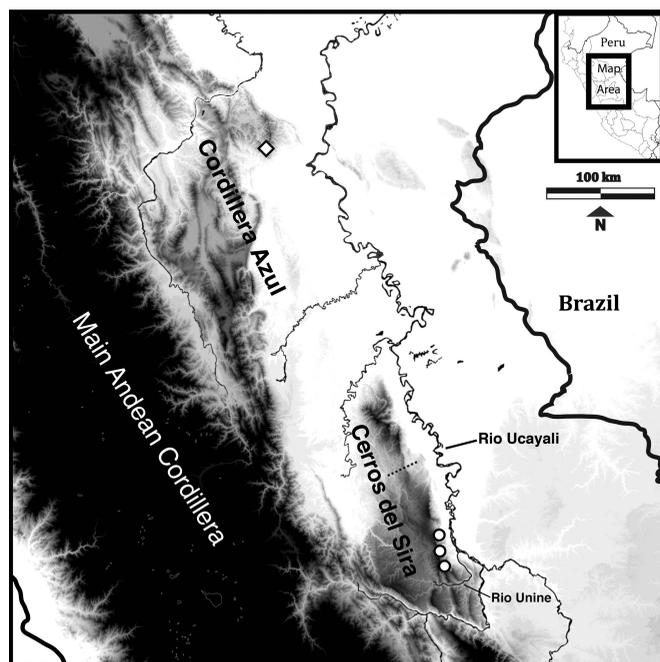


FIG. 3. Map showing all known localities for *Capito wallacei* (diamond) and *C. fitzpatricki* (circles). From south to north, *C. fitzpatricki* localities are (1) north ridge of upper Río Tzipani watershed (1,250 m), (2) north ridge of upper Río Shinipo watershed (950–1,100 m, type locality), and (3) north ridge of Quebrada Quirapokiari watershed (1,150–1,250 m). Elevation contours of 100 m are depicted by gray scale gradient. All regions of elevation >2,000 m are black; all regions <300 m are white. Dashed line divides the northern and southern portions of the Sira as defined in the text. *Capito fitzpatricki* has not been found in the portion of the Sira south of the Río Unine valley, nor in the northern portion of the Sira, despite previous surveys in these regions (see text). Its presence in the region between the known localities and the northern Sira, at appropriate habitat and elevation, is possible (this region has not been surveyed).

and moss were fairly common, and the understory was composed predominantly of low trees, shrubs, and small to medium-sized ferns. The soil surface was firm, with a relatively thin layer of decomposing leaves and detritus. Below ~950 m the forest rapidly transitioned to drier tropical lowland evergreen forest, with epiphytes and tree mosses becoming less common. In 5 days of observation, we never observed *C. fitzpatricki* below this transition zone. At the two additional localities, we observed *C. fitzpatricki* only at 1,150 m and 1,250 m in tall, lush montane forest similar to the forest on the slopes and ridge depressions at the type locality. The elevational limits of many bird species restricted to Andean montane forest coincide with transitions between montane cloud forest and tropical lowland evergreen forest (Terborgh 1985), as is likely the case with *C. fitzpatricki*.

The upper elevational limit of *C. fitzpatricki* is less clear. Thorough surveys (668 person-hours over 15 days) in dense, pristine montane forest with high moss, epiphyte, and bamboo density between 1,700 m and 2,100 m above the Río Tzipani locality did not detect *C. fitzpatricki* (Harvey et al. 2011). Surveys during four mornings by G.F.S. and colleagues in July 2011 (constituting 20 person-hours) at 1,350 m on the main ridge of the southern

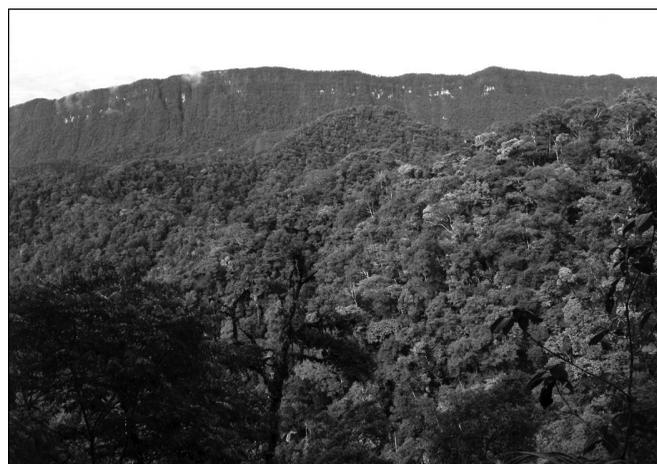


FIG. 4. Habitat of *Capito fitzpatricki* at the type locality. The species was observed in humid montane forest on the ridge-crests and slopes in the foreground (~1,100 m) but was not encountered in subtropical cloud forest between 1,700 and 2,200 m on the main ridge crest of the Sira (background). See text for discussion of habitat and elevational range.

Sira above the Quebrada Quirapokiari locality also did not detect *C. fitzpatricki*. However, it is possible that survey time spent between 1,300 m and 1,700 m at both the Tzipani and Quirapokiari localities was insufficient to determine the upper limits of *C. fitzpatricki* distribution. Therefore, the confirmed elevational distribution of *C. fitzpatricki* is 950–1,250 m, although it may range up to under 1,700 m.

Comparisons between the elevational distributions and habitats of *C. fitzpatricki* and *C. wallacei* are hindered by the limited data available. *Capito wallacei* is known from elevations between 1,250 and 1,538 m (O'Neill et al. 2000), slightly above the confirmed elevational range of *C. fitzpatricki*, and both taxa are known from montane cloud forest of varying stature. There may be differences in the forest composition and structure, and the elevation of the transition zone from montane evergreen forest and tropical lowland evergreen forest between the Cordillera Azul and the Sira. Yet analyses of ecological differentiation between the two taxa will require additional data on their distributions and a quantitative comparison of the associated habitats. Likewise, the factors that limit the distributions of both of these *Capito* species are unknown. O'Neill et al. (2000) hypothesized that *C. wallacei* occurred only above the transition to montane cloud forest in the Azul because of the presence of a congener, Gilded Barbet (*C. auratus*), just below the transition. By contrast, we found *C. fitzpatricki* and *C. auratus* to be sympatric and syntopic across the entire elevational distribution of *C. fitzpatricki* in the Sira, and we regularly observed both species feeding and using tree cavities in close proximity (see below). Therefore, it is not likely that competition or other interactions with *C. auratus* limit the elevational range of *C. fitzpatricki*.

Behavior.—We encountered *C. fitzpatricki* moving through the canopy and subcanopy, foraging in a slow, methodical manner similar to that of other *Capito*. Although generally silent, most individuals were detected by their distinctive *Tityra*-like grunts (see below). The loud, whirring wing-beats of this species also were conspicuous, as in *C. wallacei* (O'Neill et al. 2000). We observed

birds most often in pairs, although we also noted single individuals and groups of three or four. These monospecific groups accounted for the majority of our observations.

Direct foraging observations were few. On 2 November 2008, M.G.H. and G.F.S. observed a single individual in the crown of a 30-m-tall fruiting tree “reach out” (terminology from Remsen and Robinson 1990) and pluck a single berry from a fruiting branch. On 1 November 2008, B.M.W. observed a male creeping along a branch in the canopy and using its bill to probe and pick at moss or lichens. This behavior also was observed by G.F.S. on 20 July 2011 as an individual foraged in the canopy of 40-m-tall forest. An individual was observed performing bill-wiping behavior on a branch on 5 November 2008. On 23 and 27 July 2011, G.F.S. observed single individuals of *C. fitzpatricki* foraging with other frugivores, including *Aulacorhynchus derbianus*, *Tityra semifasciata*, *Pachyramphus* sp. (“*Platysaris*” group), and multiple *Tangara* spp. Both *C. wallacei* and *C. fitzpatricki* appear to be largely frugivorous, similar to other Capitonidae (Remsen et al. 1993); stomach contents of *C. fitzpatricki* consisted largely of plant matter, likely fruit, and a few insects.

M.G.H. observed one individual of *C. fitzpatricki* entering a cavity 10–12 m high in a vertical dead snag just below the crest of a ridgeline at dusk on 3 November 2008, and then vocalizing quietly (a clucking noise) several times inside. The next day, the field team took turns observing this cavity at a distance in hopes of documenting nesting behavior. At 0514 hours on 4 November 2008, one *C. fitzpatricki* was observed departing the cavity and then perching in a nearby tree for 3–4 min, where it called quietly five times. Throughout the day, two or three individuals were seen and heard near the cavity, sometimes approaching within 1–2 m of the cavity and giving clucking vocalizations. At dusk, one bird was present near the cavity but did not enter. These observations suggested that the birds were not nesting in the cavity but, rather, using it as a roost hole or potential future nest site. On 5 November 2008, we examined the cavity internally and found it to contain only wet wood shavings, with no feces, feathers, or other evidence of past or current nesting activity. The tree containing the cavity was 212 mm in diameter at the height of the roost hole. The cavity entrance hole measured 57 mm in diameter and extended 99 mm into the tree. The cavity was 298 mm deep and filled with 105 mm of wood shavings.

Vocalizations.—The limited repertoire of vocalizations we recorded for *C. fitzpatricki* consisted of two types: a *Tityra*-like grunt and a low-pitched purred song. Both were qualitatively very similar to those of *C. wallacei*. As in *C. wallacei*, the most commonly heard *C. fitzpatricki* vocalization was the *Tityra*-like grunt (e.g., LNS 138812). Most often the call sequences would alternate between a single note and a stuttered note. We often encountered pairs and recorded them giving these calls back and forth (e.g., LNS 138799). We saw one *C. fitzpatricki* lean forward, tilt its head, point its bill sharply down toward the ground, and rapidly wag its tail from side to side for the duration of its purred song, a behavior that has also been observed in *C. wallacei* (O’Neill et al. 2000). Unfortunately, because of the rarity and unpredictability of such singing bouts and the low volume and frequency, we did not obtain analyzable sound recordings of the purred song of *C. fitzpatricki*, despite intensive effort in the field (but see LNS 140635). Individuals in the roost hole gave quiet, low-pitched groans and clucks.

Phylogenetic relationships.—The phenotypic similarity between *C. fitzpatricki* and *C. wallacei* and their distinctness from

other members of the genus *Capito* suggest that these two species are sister taxa. *Capito fitzpatricki* and *C. wallacei* share the following unique characters: a red band across the breast, a scarlet crown and nape, a white supercilium, and black sides of the face (O’Neill et al. 2000). To assess relationships between *C. fitzpatricki* and *C. wallacei* and other members of the genus, we conducted a molecular phylogenetic analysis of DNA sequences collected for a larger study of the phylogenetic relationships among the Capitonidae (J. D. Weckstein et al. unpubl. data). The aligned data included 379 base pairs (bp) from the mitochondrial gene cytochrome oxidase I (COI); 1,048 bp from the mitochondrial gene cytochrome *b*; 1,041 bp from the mitochondrial gene NADH dehydrogenase subunit 2 (ND2); and 628 bp from the nuclear β -fibrinogen intron 7. Amplification and sequencing follow Armenta et al. (2005) and Patel et al. (2011), except that Capitonidae specific internal primers LbarbND2int (5’-GCYCTHGGDGGCTGGRYAGGCC-3’) and HbarbND2int (5’-GRTTGAGGCCTRYTCAGCCHCC-3’) were used for ND2. We included a number of previously published toucan and barbet DNA sequences (Armenta et al. 2005, Weckstein 2005, Patané et al. 2009, Patel et al. 2011; GenBank accession nos. AY897014–021, AY897027, AY897029–030, AY897032, AY897037, AY897042–049, AY897055, AY897057–058, AY897060, AY897065, AY959801, AY959828, AY959855, GQ457981–984, GQ458000–001, GQ458014–015, HQ424040–041, HQ424067, HQ424091, HQ424094–096, HQ424124–125). All newly generated sequences are also deposited in GenBank (JX045860–931). We analyzed phylogenetic relationships among *Capito* spp. using one individual each of *C. fitzpatricki* and *C. wallacei* and all other members of the genus (excluding *C. hypoleucus* and including multiple subspecies of *C. auratus* and *C. maculicoronatus*). For outgroups, we used *Eubucco bourcierii aequatorialis*, *E. tucinkae*, *Semnornis frantzii*, *S. ramphastinus*, *Aulacorhynchus prasinus atrogularis*, *A. prasinus caeruleogularis*, and *Andigena cucullata*. We constructed phylogenies using both maximum parsimony (MP) and Bayesian inference (BI) as implemented in PAUP* (Swofford 2002) and MRBAYES, version 3.1.2 (Ronquist and Huelsenbeck 2003), respectively. For the MP analysis, we used a heuristic search with tree-bisection-reconnection (TBR) branch swapping and 100 random addition replicates and assessed support for each node with 1,000 bootstrap replicates using a heuristic search, TBR branch swapping, and 10 random additions per replicate. For the BI analysis, we partitioned the data into a mitochondrial and a nuclear partition and used the best-fit model of molecular evolution for each partition as determined by Akaike’s information criterion scores in MRMODELTEST, version 2 (Nylander 2004); the best-fit models were GTR+I+G for the mitochondrial partition and HKY for the nuclear partition. Using these model parameters, we performed two independent BI runs of four chains for 5×10^6 generations in MRBAYES, with trees and parameters sampled every 1,000 generations, with default flat Dirichlet priors. We discarded the first 500 trees as burn-in and checked for convergence among the runs by examining the standard deviation of split frequencies between runs and the potential scale reduction factor.

The MP and BI analyses of the molecular data confirmed a sister relationship between *C. wallacei* and *C. fitzpatricki*, with strong statistical support (MP bootstrap = 100%, BI posterior probability = 1.00). Together these species are strongly supported (MP bootstrap = 100%, BI posterior probability = 1.00) as sister to a clade containing *C. brunneipectus*, *C. squamatus*,

C. maculicoronatus, and *C. auratus*. Uncorrected mtDNA *p*-distance between these *C. wallacei* and *C. fitzpatricki* individuals is 1.4%. This distance is relatively shallow with respect to pairwise uncorrected mtDNA divergence between other *Capito* species, which range from 2.2% between *C. squamatus* and *C. maculicoronatus* to 17.5% between *C. quinticolor* and *C. aurovirens*. Also, Armenta et al. (2005) found relatively higher uncorrected mtDNA divergences (4.9%) between allopatric populations of *C. auratus* that are currently considered subspecies. However, shallower mitochondrial sequence divergence has been found in taxa hypothesized to be separate species, including tropical species in two surveys of mitochondrial sequence divergences between pairs of sister species (Weir and Schluter 2004, 2007). Thus, the mitochondrial sequence divergence between *C. wallacei* and *C. fitzpatricki* is within the range of other avian sister populations that have traditionally been classified as separate species.

Phylogeographic history.—Using the same methods outlined above, we sequenced the mitochondrial genes COI and cytochrome *b* for 11 *C. wallacei* and 8 *C. fitzpatricki* individuals to further assess monophyly, divergence, and patterns of genetic diversity within and between these species. We used TCS, version 1.21 (Clement et al. 2000), to generate a statistical parsimony network and PAUP* to calculate uncorrected *p*-distances and to conduct a bootstrap analysis using a heuristic search with TBR branch swapping and 1,000 bootstrap replicates. The statistical parsimony network indicates that these two taxa are reciprocally monophyletic and divergent from one another (Fig. 5). The monophyly of these two taxa was strongly supported by MP bootstrap (100%). Uncorrected mtDNA *p*-distances averaged (mean \pm SD) $0.14 \pm 0.07\%$ (range: 0–0.21%) within *C. fitzpatricki*, $0.15 \pm 0.16\%$ (range: 0–0.42%) within *C. wallacei*, and $1.14 \pm 0.06\%$ (range: 0.98–1.33%) between the two species. Thus, these taxa are diagnosable with molecular data.

Diagnosability and heritability of plumage differences.—*Capito fitzpatricki* is 100% diagnosable from *C. wallacei* in all plumages by the presence of red flanks. Additional plumage characters reinforce this diagnosability as detailed above, yet almost all differences are associated with carotenoid pigmentation. Carotenoids cannot be synthesized by birds and must be consumed and

assimilated into growing feathers (Brush 1978, McGraw 2006). The proximate basis for carotenoid plumage variation has been most intensively studied in the House Finch (*Carpodacus mexicanus*, Fringillidae, Passeriformes). In this species, hue (yellow to red) is governed by the amount of specific red-pigment carotenoids in their diet (Hill 1992), yet the patterning of their carotenoid plumage is highly heritable (Hill 1993). By contrast, diet manipulations of the Northern Flicker (*Colaptes auratus*, Picidae, Piciformes, which includes Capitonidae) revealed carotenoid pigmentation and patterning of wing and tail feathers to be genetically determined (Test 1969). Furthermore, in both Picidae and the Northern Cardinal (*Cardinalis cardinalis*, Cardinalidae, Passeriformes), yellow carotenoids in the diet are directly assimilated into the feathers, whereas the genetically governed metabolism of these same yellow carotenoids produces red pigments (Stradi et al. 1998, McGraw et al. 2003). If differences in diet were solely responsible for the differences in flank coloration between *C. fitzpatricki* and *C. wallacei*, one would expect all red-pigmented areas to be affected to the same degree as the flanks. Both *C. fitzpatricki* and *C. wallacei*, however, show similar red coloration on the crown, nape, back, and breast, though more extensive on the back in *C. fitzpatricki*. Assuming that genetic control of the patterning and metabolism of red pigments is conserved across Piciformes, the differences in carotenoid coloration between *C. fitzpatricki* and *C. wallacei* likely indicate additional underlying genetic differences between these species (McGraw et al. 2003).

Morphological diagnosability.—To assess the morphological distinctiveness and diagnosability of *C. fitzpatricki* and *C. wallacei*, we conducted a morphometric analysis using principal component analysis (PCA), multivariate analysis of variance (MANOVA), and discriminant function analysis. G.F.S. measured standard morphological measurements of culmen, wing, tail, tarsus length, and bill depth from both species, using digital calipers on all specimens that were prepared as round skins (Table 1), excluding the single presumed subadult male of *C. fitzpatricki* (AU-CORBIDI 2795). We log-transformed all values, and assumptions of univariate and multivariate normal error and homogeneity of variances were met. Single morphological variables were not measured on two specimens because of damage. For the multivariate analyses, we predicted these missing values using a multiple regression of measurements from individuals with complete data from the specimen's respective population. We found no effect of sex on the morphometric data (MANOVA) either within populations ($F = 0.92$, $df = 5$ and 12 , $P = 0.50$) or pooled ($F = 1.44$, $df = 5$ and 12 , $P = 0.28$); therefore, we combined sexes for each population in subsequent multivariate analyses.

The PCA resulted in two main axes, which described 79% of the variation seen within both species (Fig. 6). The first principal component (PC1) recovered two clusters at either extreme, representing *C. wallacei* and *C. fitzpatricki* (Fig. 6). This axis primarily reflects the greater bill depth of *C. fitzpatricki* but is also positively correlated with generally longer tarsus and wing measurements (PC1 loadings: culmen: 0.10, wing: 0.16, tail: 0.06, tarsus: 0.38, bill depth: 0.90). The second principal component (PC2) reflects the variation in tarsus length but does not contribute to separation of the species (Fig. 6; PC2 loadings: culmen: 0.07, wing: 0.13, tail: –0.34, tarsus: 0.85, bill depth: –0.37). We found that the PCA segregation of *C. wallacei* and *C. fitzpatricki* was significant in a MANOVA ($F = 21.54$, $df = 5$ and 14 , $P < 0.001$). A discriminant function analysis

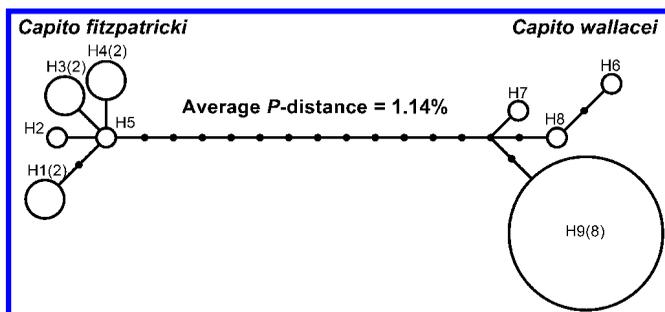


FIG. 5. The mtDNA haplotype network of all *Capito fitzpatricki* and *C. wallacei* samples in the study showing a cluster of haplotypes for each species. The haplotypes in these species-specific haplotype clusters differ by an average *p*-distance of 1.14%. Each line segment represents a single mutational step; solid circles indicate unsampled haplotypes. The size of each open circle is proportional to the total number of samples with the corresponding haplotype (H#), and the number in parentheses indicates the number of samples carrying that haplotype.

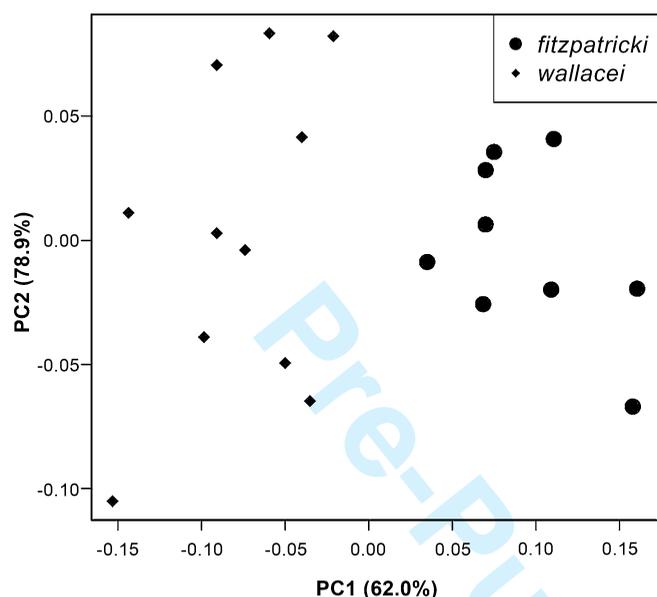


FIG. 6. Factor scores from principal component analysis of five morphological variables of *Capito fitzpatricki* and *C. wallacei* showing the sister taxa to be morphologically segregated. Cumulative proportion of the total variance explained by principal components (PC) 1 and 2 are in parentheses beside axis labels.

recovered a single linear combination of the morphological variables that correctly assigned all specimens to their respective species. Wing length and bill depth were the most heavily weighted coefficients, whereas the four other variables contributed relatively little (coefficients of LD1: culmen: -11.06 , wing: 29.25 , tail: -2.77 , tarsus: 2.64 , bill depth: 26.18). Variation in specimen preparation is unlikely to bias measurements because specimens of both species were prepared by several preparators and, thus, any associated biases should be equally distributed among both of the series. These analyses demonstrate that *C. wallacei* and *C. fitzpatricki* are morphologically distinct and diagnosable.

Species status criteria.—As detailed above, *C. wallacei* and *C. fitzpatricki* are allopatric sister taxa that are 100% diagnosable using genetic characters (mtDNA), plumage, and morphology. Therefore, these taxa should be considered species on the basis of the phylogenetic species concept (Cracraft 1983). The low mitochondrial sequence divergence suggests that they have differentiated relatively recently, but this divergence is within the range of divergence found between avian sister species (Weir and Schluter 2004, 2007). As is the case with the majority of allopatric taxa, data from *C. fitzpatricki* and *C. wallacei* are insufficient to infer whether or not they can interbreed, and we are not aware of any data on reproductive isolation in similarly divergent taxa within or closely related to Capitonidae, most of which are also allopatrically distributed. Therefore, reproductive isolation (a criterion of the biological species concept) cannot be evaluated. Additional research into reproductive isolating mechanisms in Capitonidae, aside from geographic isolation, is warranted.

Conservation.—The species occurs in a narrow elevational zone on the boundary of, and within, the Sira Communal Reserve. Its proximity to this communal reserve affords some protection, as does the steep topography and current lack of roads in the Sira,

which limit the montane forest's exposure to human influence. Nevertheless, mining, logging, and oil exploration are active in the region and threaten the montane forests. Also, the effects of climate change on such habitats could represent a threat over the longer term (e.g., Forero-Medina et al. 2011). This species is known only from a very small range (<300 km²), where it is likely found continuously at appropriate elevations. Its total range may be <700 km² if it does not occur on the western slope or northern portion of the Sira. Thus, this species could be considered endangered or vulnerable by the International Union for Conservation of Nature (IUCN 2001). Habitat-loss risk estimates and demographic data are needed for further evaluation of conservation status.

ACKNOWLEDGMENTS

We are grateful for the assistance of our Ashéninka guides in the field. The hospitality of the communities of the Organización Ashéninka del Gran Pajonal, Organización Indígena Regional de Atalaya, and Asociación Regional de Pueblos Indígenas will be warmly remembered. We thank the Dirección General Forestal y de Fauna Silvestre of Peru (R. D. no. 281-2011-AG-DGFFS-DGEFFS) for permission to collect specimens in the region. A. T. Peterson and M. B. Robbins (KUNHM), K. S. Bostwick (CUMV), T. Valqui (CORBIDI), and G. F. Budney (ML) were generous in support of logistical aspects of the collecting and recording efforts and with advice on many aspects of the field work. We thank I. J. Lovette, D. W. Winkler, and numerous staff members at the Cornell Lab of Ornithology for providing all manner of support throughout the planning stages of the 2008 expedition, and L. R. Cancino for providing logistical support in Lima. D. F. Lane freely gave of his firsthand observations and knowledge of *C. wallacei*. We thank R. S. Terrill for his field contributions, G. A. Bravo, A. M. Cuervo, and the Louisiana State University and Field Museum bird groups for their expertise and advice during preparation of the manuscript. J. W. Fitzpatrick and J. P. O'Neill helped provide the initial spark to undertake this project, and T.S. Schulenberg was incredibly supportive throughout both expeditions. J. M. Bates, D. F. Lane, J. V. Remsen, Jr., and three anonymous reviewers made helpful comments that improved the manuscript. This work was supported by the Cornell Lab of Ornithology, National Geographic Society, Explorer's Club, Coypu Foundation, the Rawlings Cornell Presidential Research Scholars, Jordani Zoology Club, Eastern Mountain Sports, National Science Foundation DEB-0515672 and DEB-1120054 to J.D.W., and the Field Museum's Emerging Pathogens Project funded by the Davee Foundation and the Dr. Ralph and Marian Falk Medical Research Trust. DNA sequencing was carried out at the Field Museum's Pritzker Laboratory for Molecular Systematics and Evolution, operated with support of the Pritzker Foundation.

LITERATURE CITED

- ARMENTA, J. K., J. D. WECKSTEIN, AND D. F. LANE. 2005. Geographic variation in mitochondrial DNA sequences of an Amazonian nonpasserine: The Black-spotted Barbet complex. *Condor* 107:527–536.
- BRUSH, A. H. 1978. Avian pigmentation. Pages 141–161 in *Chemical Zoology*, vol. 10: Aves (A. Brush, Ed.). Academic Press, New York.

- CLEMENT, M., D. POSADA, AND K. A. CRANDALL. 2000. TCS: A computer program to estimate gene genealogies. *Molecular Ecology* 9:1657–1660.
- CRACRAFT, J. 1983. Species concepts and speciation analysis. Pages 159–187 in *Current Ornithology*, vol. 1 (R. F. Johnston, Ed.). Plenum Press, New York.
- FITZPATRICK, J. W., AND J. P. O'NEILL. 1979. A new tody-tyrant from northern Peru. *Auk* 96:443–447.
- FITZPATRICK, J. W., AND J. P. O'NEILL. 1986. *Otus petersoni*, a new screech-owl from the eastern Andes, with systematic notes on *O. colombianus* and *O. ingens*. *Wilson Bulletin* 98:1–14.
- FITZPATRICK, J. W., AND D. F. STOTZ. 1997. A new species of tyrannulet (*Phylloscartes*) from the Andean foothills of Peru and Bolivia. Pages 37–44 in *Studies in Neotropical Ornithology Honoring Ted Parker* (J. V. Remsen, Jr., Ed.). *Ornithological Monographs*, no. 48.
- FITZPATRICK, J. W., J. W. TERBORGH, AND D. E. WILLARD. 1977. A new species of wood-wren from Peru. *Auk* 94:195–201.
- FITZPATRICK, J. W., AND D. E. WILLARD. 1990. *Cercomacra manu*, a new species of antbird from southwestern Amazonia. *Auk* 107:239–245.
- FITZPATRICK, J. W., D. E. WILLARD, AND J. W. TERBORGH. 1979. A new species of hummingbird from Peru. *Wilson Bulletin* 91:177–186.
- FORERO-MEDINA, G., J. TERBORGH, S. J. SOCOLAR, AND S. L. PIMM. 2011. Elevational ranges of birds on a tropical montane gradient lag behind warming temperatures. *PLoS One* 6:e28535.
- GASTAÑAGA, M., A. B. HENNESSEY, AND R. MACLEOD. 2007. Rediscovery of Southern Horned Curassow, *Pauxi unicornis koepckeae*, in Cerros del Sira, Peru. *Cotinga* 28:63–66.
- GRAVES, G. R., AND J. S. WESKE. 1987. *Tangara phillipsi*, a new species of tanager from the Cerros del Sira, eastern Peru. *Wilson Bulletin* 99:1–6.
- HARVEY, M. G., B. M. WINGER, G. F. SEEHOLZER, AND D. CÁCERES. 2011. Avifauna of the Gran Pajonal and southern Cerros del Sira, Peru. *Wilson Journal of Ornithology* 123:289–315.
- HILL, G. E. 1992. Proximate basis of variation in carotenoid pigmentation in male House Finches. *Auk* 109:1–12.
- HILL, G. E. 1993. Geographic variation in the carotenoid plumage pigmentation of male House Finches (*Carpodacus mexicanus*). *Biological Journal of the Linnean Society* 49:63–86.
- IUCN. 2001. IUCN Red List Categories and Criteria, version 3.1. IUCN Species Survival Commission. IUCN, Gland, Switzerland, and Cambridge, United Kingdom
- KRABBE, N., D. J. AGRO, N. H. RICE, M. JACOME, L. NAVARRETE, AND F. SORNOZA M. 1999. A new species of antpitta (Formicariidae: *Grallaria*) from the southern Ecuadorian Andes. *Auk* 116:882–890.
- LANE, D. F., G. P. SERVAT, T. VALQUI H., AND F. R. LAMBERT. 2007. A distinctive new species of tyrant flycatcher (Passeriformes: Tyrannidae: *Cnipodectes*) from southeastern Peru. *Auk* 124:762–772.
- MCGRAW, K. J. 2006. The mechanics of carotenoid coloration. Pages 177–242 in *Bird Coloration*, vol. 1: Mechanisms and Measurements (G. E. Hill and K. J. McGraw, Eds.). Harvard University Press, Cambridge, Massachusetts.
- MCGRAW, K. J., G. E. HILL, AND R. S. PARKER. 2003. Carotenoid pigments in a mutant cardinal: Implications for the genetic and enzymatic control mechanisms of carotenoid metabolism in birds. *Condor* 105:587–592.
- MEE, A., J. OHLSON, I. STEWART, M. WILSON, P. ÖRN, AND J. DIAZ FERREYRA. 2002. The Cerros del Sira revisited: Birds of submontane and montane forest. *Cotinga* 18:46–57.
- NYLANDER, J. A. A. 2004. MrModelTest, version 2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden.
- O'NEILL, J. P., D. F. LANE, A. W. KRATTER, A. P. CAPPARELLA, AND C. F. JOO. 2000. A striking new species of barbet (Capitoninae: *Capito*) from the eastern Andes of Peru. *Auk* 117:569–577.
- PATANÉ, J. S. L., J. D. WECKSTEIN, A. ALEIXO, AND J. M. BATES. 2009. Evolutionary history of *Ramphastos* toucans: Molecular phylogenetics, temporal diversification, and biogeography. *Molecular Phylogenetics and Evolution* 53:923–934.
- PATEL, S., J. D. WECKSTEIN, J. S. L. PATANÉ, J. M. BATES, AND A. ALEIXO. 2011. Temporal and spatial diversification of *Pteroglossus arcaaris* (Aves: Ramphastidae) in the Neotropics: Constant rate of diversification does not support a Pleistocene radiation. *Molecular Phylogenetics and Evolution* 58:105–115.
- REMSEN, J. V., JR., M. A. HYDE, AND A. CHAPMAN. 1993. The diets of Neotropical trogons, motmots, barbets and toucans. *Condor* 95:178–192.
- REMSEN, J. V., JR., AND S. K. ROBINSON. 1990. A classification scheme for foraging behavior of birds in terrestrial habitats. Pages 144–160 in *Avian Foraging Theory, Methodology, and Applications* (M. L. Morrison, C. J. Ralph, J. Verner, and J. R. Jehl, Jr., Eds.). *Studies in Avian Biology*, no. 13.
- RIDGWAY, R. 1912. *Color Standards and Color Nomenclature*. Published by the author, Washington, D.C.
- RONQUIST, F., AND J. P. HUELSENBECK. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572–1574.
- STRADI, R., J. HUDON, G. CELENTANO, AND E. PINI. 1998. Carotenoids in bird plumage: The complement of yellow and red pigments in true woodpeckers (Picinae). *Comparative Biochemistry and Physiology B* 120:223–230.
- SWOFFORD, D. L. 2002. PAUP*: Phylogenetic Analysis Using Parsimony (*and Other Methods), version 4.0b10. Sinauer Associates, Sunderland, Massachusetts.
- TERBORGH, J. 1985. The role of ecotones in the distribution of Andean birds. *Ecology* 66:1237–1246.
- TERBORGH, J., AND J. S. WESKE. 1975. The role of competition in the distribution of Andean birds. *Ecology* 56:562–576.
- TEST, F. H. 1969. Relation of wing and tail color of the woodpeckers *Colaptes auratus* and *C. cafer* to their food. *Condor* 71:206–211.
- WECKSTEIN, J. D. 2005. Molecular phylogenetics of the *Ramphastos* toucans: Implications for the evolution of morphology, vocalizations, and coloration. *Auk* 122:1191–1209.
- WEIR, J. T., AND D. SCHLUTER. 2004. Ice sheets promote speciation in boreal birds. *Proceedings of the Royal Society of London, Series B* 271:1881–1887.
- WEIR, J. T., AND D. SCHLUTER. 2007. The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science* 315:1574–1576.
- WESKE, J. S., AND J. W. TERBORGH. 1971. A new subspecies of curassow of the genus *Pauxi* from Peru. *Auk* 88:233–238.
- WESKE, J. S., AND J. W. TERBORGH. 1977. *Phaethornis koepckeae*, a new species of hummingbird from Peru. *Condor* 79:143–147.

Associate Editor: J. Klicka