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Source: The Wilson Journal of Ornithology, 126(2):179-191. 2014.

Published By: The Wilson Ornithological Society

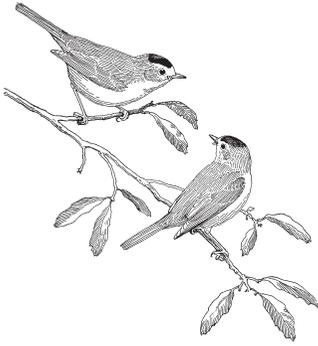
DOI: <http://dx.doi.org/10.1676/13-135.1>

URL: <http://www.bioone.org/doi/full/10.1676/13-135.1>

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The Wilson Journal of Ornithology

Published by the Wilson Ornithological Society

VOL. 126, NO. 2

June 2014

PAGES 179–416

The Wilson Journal of Ornithology 126(2):179–191, 2014

THE AVIAN BIOGEOGRAPHY OF AN AMAZONIAN HEADWATER: THE UPPER UCAYALI RIVER, PERU

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ABSTRACT.—The Ucayali River is a major tributary of the Amazon, but it narrows considerably toward its headwater at the base of the Andes. This region, the upper Ucayali Valley, is of biological interest for the large number of closely related birds elsewhere separated from each other by major rivers that come into close proximity and potential contact. Between 2006–2011, we conducted the first modern ornithological inventory of the upper Ucayali River and sampled localities in all major avian habitats on either side of the river. We document the continued importance of the Ucayali River

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as a biogeographic barrier, even at the headwater, but also find that some mixing occurs, both in the form of taxa crossing to the “wrong” bank and in the potential intergradation of distinct forms. We describe the biogeography of birds in the region, characterize the avifaunas of major habitats, and discuss in detail species of particular biogeographical interest. Received 25 August 2013. Accepted 10 January 2014.

Key words: Amazonia, biogeography, range extension, river barrier, river island, Ucayali, white sand.

The rivers of the Amazon Basin are important barriers to the distributions of terrestrial animals (Wallace 1852), even for relatively vagile taxa such as birds (Sick 1967, Haffer 1969). The narrowing of rivers in their headwaters regions, however, may result in the mixing of faunas and potential contact between otherwise geographically separated forms (Wallace 1852, Haffer 1992, Bates et al. 2004, Naka et al. 2012). The Ucayali River is a major headwater tributary of the Amazon River, but narrows to roughly 0.5 km in width in its uppermost reaches at the base of the Andes Mountains. The upper Ucayali River lies near the intersection of the Napo and Inambari areas of endemism (Cracraft 1985) and in an area with many distributional limits (Schulenberg et al. 2010). Therefore, it is a potential zone of contact between divergent populations or species separated downstream by the greater breadths of the lower Ucayali and Amazon rivers.

Avian distributional limits along the upper Ucayali River are unclear, because little ornithological work has been conducted in the region. Most information on the regional avifauna comes from the collections of Alfonso and Ramón Olalla, who worked on the uppermost Ucayali River for Frank M. Chapman and the American Museum of Natural History (AMNH) during 1927–1928. Accusations that the Olallas falsified specimen data arose in the 1960s, but a recent analysis suggests that much of their locality information is reliable and that their collections should be useful for biogeographical studies (Wiley 2010). No other work has been conducted on the upper Ucayali River since the 1920s, although expeditions have been made nearby to the Pucallpa area and Sierra del Divisor to the north (O’Neill and Pearson 1974, O’Neill et al. 1991, Whitney et al. 2004, Schulenberg et al. 2006a, Srinivas and Molina Vilca 2013), the Pachitea Valley and highlands of the Sira Mountains to the west (Weske 1972, Terborgh and Weske 1975, González M. 1998, Harvey et al. 2011, Socolar et al. 2012), the Urubamba River and slopes of the Vilcabamba Mountains to the south (Schulenberg 2001; M. J. Miller unpubl. data), and Balta in the Purus drainage well to the east (O’Neill 1969).

We present the results of the first modern ornithological surveys of the region surrounding the upper Ucayali River, including sites on both banks. We examine the influence of the upper Ucayali River on bird distributions and compare distributional patterns from this area to patterns based on prior fieldwork downriver along the middle Ucayali. We describe the bird communities of major habitats, and provide details on species of particular biogeographical interest. We compare our results to the Olalla collections and discuss the validity of their data and comment on the conservation importance of the region. We include a species list annotated with information on distribution, abundance, habitat, and status in the online Supplemental Material.

METHODS

Study Region

The upper Ucayali River forms at the confluence of the Tambo and Urubamba rivers and then flows northward along the eastern base of the Cerros del Sira (Fig. 1). The upper Ucayali River sits in a broad valley bounded to the west by the Cerros del Sira and to the east by hilly terrain extending to the upper Juruá River near the Brazil border. The valley of the upper Ucayali River comprises much of the western portion of the Region (formerly Department) of Ucayali. The climate is wet and hot, with mean annual rainfall of 2,950 mm and a mean annual temperature of 25 °C at Atalaya near the confluence of the Tambo, Urubamba, and Ucayali rivers (Oficina Nacional de Evaluación de Recursos Naturales 1968). The valley contains a diverse array of lowland Amazonian and Andean foothill habitats, several of which are important for ecologically specialized bird species. *Terra firme* forest is extensive in upland areas, and *várzea*-like floodplain forest is widespread on the alluvial plain of the whitewater Ucayali River and major tributaries. *Igapó*-like floodplain forest is localized around blackwater streams and *cochas*, or oxbow lakes. Stunted forest on sandy soil that resembles white sand forest (*varillal*) is very restricted in the region but occurs in a few small patches to the east of the alluvial plain of the Ucayali River.

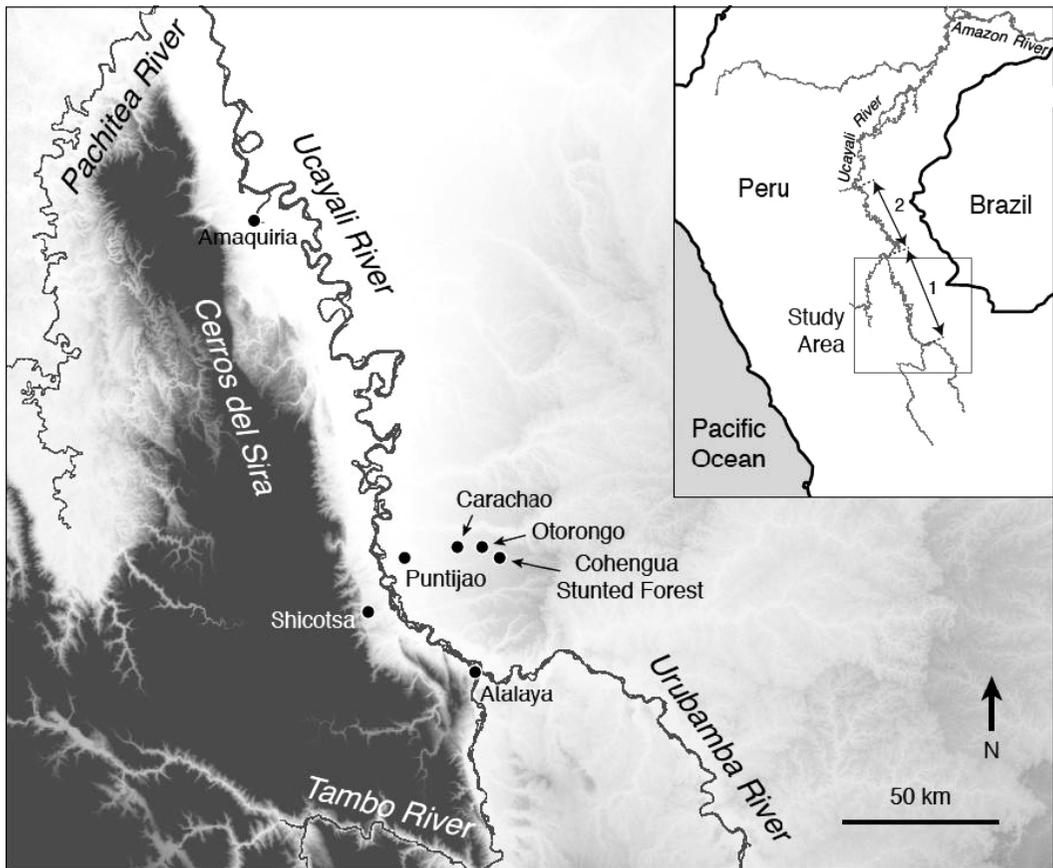


FIG. 1. A map of the study area showing the locations of primary study sites mentioned in the text. Numbers in the inset refer to sections of the Ucayali River used in the biogeographic analyses: (1) upper Ucayali River and (2) middle Ucayali River.

Lowland *Guadua* spp. bamboo occurs in small stands along the base of the Sira and may also occur in very large stands in the uplands well to the east of the Ucayali River. Palm swamps of *Mauritia* spp. occur in poorly drained locations throughout the area, including within the stunted forest. River edges and islands harbor a suite of successional habitats, and successional habitats also occur around the edges of the town of Atalaya and various indigenous communities. Along the eastern base of the Sira, the forest transitions gradually into lower montane evergreen forest between ~500–900 m.

Study Sites

The authors surveyed the region of the upper Ucayali River on a total of 160 days during six visits between 2006–2011 (Table 1). Inventory sites are scattered across the valley on both sides of the river (Fig. 1).

The Ucayali River is a meandering whitewater river that contains numerous islands and sandbars. River level fluctuates widely with season, and fallen trees and debris as well as the predominance of secondary habitat are evidence of fluvial effects on the landscape. For our purposes, this site contains all areas in and immediately adjacent to the river, including islands. Sampling effort was scattered along the river, although we made an effort to intensively sample an island in the mouth of the Tambo River ($10^{\circ} 71' S, 73^{\circ} 76' W$; 210 m). Habitats on this island were typical of other younger islands in the area and included sandy flats, *Gynerium* spp. cane, *Tessaria* spp. scrub, and *Cecropia* spp.-dominated woodland.

Puntijao ($10^{\circ} 41' S, 73^{\circ} 95' W$; 200 m) is a camp alongside the Quebrada Puntijao in the alluvial plain of the Ucayali River 7 km to the east of the river itself. Habitat here is primarily várzea-like floodplain forest, although igapó-like

TABLE 1. Sampling effort between 2006–2011 at study sites in the upper Ucayali Valley, Peru.

Site	Institutions	Habitats surveyed ^a	Dates surveyed	Surveyors	Species detected
Puntijao	CORBIDI, LSUMINS	V, C, W, R	19–25 June 2011	MGH, GFS, DCA, FHC, MAAJ, CVD, SFR, RST, CEB	237
Carachao	CORBIDI, LSUMINS	T, C	24–29 May 2011	MGH, GFS, DCA, FHC, MAAJ, CVD, SFR, RST, CEB	185
Otorongo	CORBIDI, LSUMINS	T, M	30 May–18 June 2011	MGH, GFS, DCA, FHC, MAAJ, CVD, SFR, RST, CEB	222
Cohengua Stunted Forest	CORBIDI, LSUMINS	S, T, M	2, 10–14 June 2011	MGH, GFS, DCA, FHC, MAAJ, CVD, SFR, RST, CEB	100
Ucayali River	CORBIDI, LSUMINS	R, I	Various dates in 2006, 2008, 2010, and 2011	All authors	139
Atalaya vicinity	CORBIDI, LSUMINS	T, V, C, R, W	Various dates in 2006, 2008, 2010, and 2011	MGH, GFS, DCA, BMW, FHC, MAAJ, CVD, SFR, RST, CEB, LAAL, GB, MC, OC, OB	306
Shicotsa	CORBIDI, LSUMINS	T, V, B, C, R	Various dates in 2008 and 2011	MGH, GFS, DCA, BMW, FHC, MAAJ, CVD, SFR, RST, GB, OC	248
Amaquiria	CORBIDI, AMNH	T, C, V, R	11–31 August 2009	JGT, SFR, LAAL, AQZ, AUT, WAGB, AZS, FWPR, WMM	295

^a T = humid upland forest (*terra firme*), V = humid bottomland forest (*várzea* and *igapó*), S = stunted forest, C = clearings and successional areas, I = river islands, R = river and river edge, B = *Guadua* spp. bamboo, M = *Mauritia* spp. palm swamps, W = wetlands, O = overhead.

floodplain forest is present along the blackwater Quebrada Puntijao as well as around a large *cocha* (10° 40' S, 73° 97' W; 200 m). Successional habitats are present around the Ashéninka community of Galilea on the bank of the Ucayali (10° 44' S, 74° 01' W; 200 m) and along a logging road running close to camp.

Carachao (10° 38' S, 73° 80' W; 280 m) is a logging camp in uplands 24 km to the east of the Ucayali River. Habitat here is selectively logged, tall *terra firme* forest. Several *Mauritia* swamps are in the vicinity, and successional habitats are present in clear-cuts near the village of Chorinashi (10° 34' S, 73° 78' W; 270 m) to the north.

Otorongo (10° 38' S, 73° 73' W; 350 m) is a logging camp located in uplands 32 km to the east of the Ucayali River. Habitat is tall *terra firme* forest with a more open canopy than the forest at Carachao because of selective logging. A blackwater stream, Quebrada Yanayacu, lined with *Mauritia* palms, is located 2 km to the east of camp (10° 38' S, 73° 71' W; 340 m). Forest to the east of camp transitions gradually to stunted forest.

The Cohengua Stunted Forest (10° 41' S, 73° 68' W; 370 m) is an area of scrub and short-stature forest on poorly drained, sandy soil 36 km east of the Ucayali River. A gradual transition occurs from tall (30+ m) *terra firme* forest in the vicinity of Otorongo to shorter forest (10–20 m) and finally scrub and grassland in the center of the Cohengua Stunted Forest. Low-lying areas are often flooded and are dominated by grasses and *Mauritia* palms. Small blackwater streams are located throughout.

Atalaya (10° 73' S, 73° 75' W; 220 m), the only town in the upper Ucayali Valley, is on the Tambo River just above its confluence with the Urubamba River. Pastures and scrub surround the town and patches of *terra firme* and *várzea*-like floodplain forest occur on the outskirts. Ridges west of town contain forest that transitions to lower montane evergreen forest. Survey effort was concentrated around Atalaya itself as well as at Canuja (10° 79' S, 73° 77' W; 240–450 m), an Ashéninka community and hydroelectric facility located just over the border into Junín Region 6 km south of Atalaya.

Shicotsa (10° 44' S, 74° 10' W; 320 m) is a camp along the Quebrada Shicotsa near the Ashéninka community of Pennsylvania. The camp is at the base of the Cerros del Sira 8 km west of the Ucayali River. Habitat here is dominated by tall *terra firme* forest on hilly terrain, with a

gradual transition to lower montane evergreen forest with increasing elevation. A patch of *Guadua* spp. bamboo is located along the top of a small ridge at the base of the slopes of the Cerros del Sira. We include in this site observations from nearby areas between Shicotsa and Misión Unine (10° 64' S, 73° 97' W; 250 m) to the south that were of similar habitat and terrain and that were sampled opportunistically during visits to higher elevations.

Amaquiria (9° 46' S, 74° 38' W; 170 m) is a Shipibo-Conibo native community located at the west bank of the Tipishca Amaquiria River in the Reserva Comunal El Sira. Habitat along the river margins here includes successional vegetation dominated by *Tessaria* spp. and river and forest edge vegetation bordering the community. We also treat as part of this site, two other camps in the same area: Sipiria (9° 47' S, 74° 44' W; 173 m) on the west side of Quebrada Sipiria at Puesto de Vigilancia No.1 in the Reserva Comunal El Sira, with habitats dominated by tall *terra firme* forest, *várzea*-like forest, and some clearings and successional habitats; and Tambo (9° 47' S, 74° 48' W; 250–500 m), on the west side of Quebrada Tambo in the Reserva Comunal El Sira at the base of the Cerros del Sira with tall *terra firme* forest transitioning rapidly to lower montane evergreen forest with increasing elevation.

Fieldwork

We conducted observational surveys along transects that followed logging tracks, trails, or water courses between 0500–1200 PET and often again between 1400–1830. We tallied all birds seen or heard, recorded habitat associations, made audio recordings, and collected birds using shotguns and mist-nets. Observation data were deposited in the Avian Knowledge Network through the eBird portal, Cornell Laboratory of Ornithology, Ithaca, New York, USA. We archived audio recordings at the Macaulay Library (ML), Cornell Laboratory of Ornithology. Voucher specimens and tissue samples were deposited at the Centro de Ornitología y Biodiversidad (CORBIDI), Lima, Peru; the Louisiana State University Museum of Natural Science (LSUMNS), Baton Rouge, Louisiana, USA; and the American Museum of Natural History (AMNH), New York, USA. Birds were identified to species using the taxonomy of the South American Classification Committee of the American Ornithologist's Union (Ramsen et al. 2013). Where possible, birds were

further identified to subspecies using the taxonomy of Dickinson (2003) and Dickinson and Ramsen (2013).

Distributional Analyses

In order to investigate the relative importance of the upper Ucayali River as a biogeographic barrier, we compared species distributions based on our inventory results along the upper Ucayali to records along the middle Ucayali River based on compilations of existing distributional data from this relatively well-sampled region (Parker et al. 1996; Ridgely et al. 2003; Schulenberg et al. 2006b, 2010). We define the upper Ucayali as the stretch of river between the confluence of the Tambo and Urubamba Rivers and the mouth of the Pachitea River, and the middle Ucayali as the stretch between the mouth of the Pachitea River and the mouth of the Pauya River near the Cordillera Azul (Fig. 1). For both the upper and middle Ucayali, we generated a list of pairs of closely related species that are separated by the river. We did not include the lower Ucayali River in this analysis because the bird life in that region is poorly known, and because the course of the Ucayali in that region is known to have undergone frequent shifts (Dumont 1991) that may have allowed species pairs to mix (Tuomisto and Ruokolainen 1997).

We did not include subspecies in the distributional analysis of the upper and middle Ucayali River because the subspecific taxonomy of many Amazonian species is in need of revision (Ramsen et al. 2013). We were interested in the role of the upper Ucayali River in structuring intraspecific diversity, however, and we examined our results from the upper Ucayali to determine which species contained multiple phenotypically diagnosable forms within the study area. If possible, we assigned these forms to subspecies based on the taxonomy of Dickinson (2003) and Dickinson and Ramsen (2013). We stress that subspecies assignments should be considered preliminary and are used here as a convenience absent an alternative means of describing the observed intraspecific variation.

RESULTS

We recorded 564 bird species representing 66 families below 900 m elevation in the study region, 393 of which were documented with specimens or audio recordings. Species recorded above 900 m elevation during our surveys are

TABLE 2. Species pairs with distributions that are limited by either the upper or middle Ucayali River.

Genus	West bank species	East bank species	Limited by middle Ucayali? ^a	Limited by upper Ucayali? ^b	Species crossing river
<i>Galbula</i>	<i>albirostris</i>	<i>cyanicollis</i>	Yes	Yes	-
<i>Malacoptila</i>	<i>fusca</i>	<i>semicineta</i>	Yes	Yes	-
<i>Nonnula</i>	<i>brunnea</i>	<i>sclateri</i>	Yes	No	<i>sclateri</i>
<i>Picumnus</i>	<i>lafresnayi</i>	<i>aurifrons</i>	Yes	Yes	-
<i>Pionites</i>	<i>melanocephalus</i>	<i>leucogaster</i>	Yes	No	<i>leucogaster</i>
<i>Frederickena</i>	<i>fulva</i>	<i>unduliger</i>	Yes	Yes	-
<i>Gymnopathys</i>	<i>lunulatus</i>	<i>salvini</i>	Yes	No	<i>salvini</i>
<i>Hemitriccus</i>	<i>zosterops</i>	<i>griseipectus</i>	Yes	Unknown	-
<i>Pheugopedius</i>	<i>coraya</i>	<i>genibarbis</i>	Yes	No	see text

^a Based on Parker et al. (1996), Ridgely et al. (2003), Schulenberg et al. (2006b), and Schulenberg et al. (2010).

^b Based on results from this inventory.

discussed in Harvey et al. (2011). We recorded 455 species west of the Ucayali River, 382 species east of the Ucayali River, and 139 species on the river itself, including on river islands. Five hundred and three of the species observed are Amazonian residents, and the remainder are species distributed primarily in the Andes or vagrants from elsewhere. Twenty-one species of austral migrants and 21 species of boreal migrants were recorded. Of the Amazonian residents, 462 are present on both sides of the Amazon River, nine are species that are primarily northern Amazonian (north of the Amazon River) in distribution (based on Parker et al. 1996), and 32 are species that are primarily southern Amazonian. Additional information on distribution among the study sites, relative abundance, habitat, documentation, migratory status, and biogeographic affinities for each species and subspecies identified is in the online Supplemental Material.

Biogeography and the Ucayali River

We found the middle Ucayali River serves as a distributional break to nine species pairs (Table 2). In contrast, the upper Ucayali River within our study area delimits only four pairs, all of which are delimited by the middle Ucayali River. Sufficient distributional data from the upper Ucayali River are lacking for one pair that is delimited by the middle Ucayali. Of the four species pairs that are not delimited by the upper Ucayali River, in three the species typically found on the east bank also occurs on the west bank. In the fourth species pair not delimited by the upper Ucayali River, the details of the distribution of both species are unclear because of the presence of individuals with intermediate phenotypes.

Further scrutiny of variation within species revealed 11 species in which two diagnosable forms were present within the study area (Table 3). Eight of the 11 pairs of diagnosable forms appeared, based on our records, to be delimited by the Ucayali River. We observed phenotypic evidence of introgression in two subspecies pairs and one species pair that are sufficiently distinct phenotypically to recognize intermediates. Black-necked Stilt (*Himantopus mexicanus*) individuals present along the upper Ucayali River variously resembled either the black-backed *H. m. mexicanus* or white-backed *H. m. melanurus*, and some had apparent intermediate shades of gray on the back and hindneck. On the west side of the Ucayali River, Blue-crowned Manakin (*Lepidothrix coronata*) resembled the green-bodied form *L. c. exquisita*, distributed west of the Ucayali north to the Marañon. Individuals on the east side of the Ucayali River, however, were various shades of greenish-black and appeared to be intermediate between the black-bodied form *L. c. coronata* found east of the Ucayali River and a green-bodied form, either *L. c. exquisita* or *L. c. caelestipileata* of southeastern Peru. Members of the Coraya (*Pheugopedius coraya*) and Whiskered (*P. genibarbis*) Wren species pair along the upper Ucayali River are highly variable in plumage, but many appear intermediate between the two species.

Habitat Associations

Birds of Terra Firme Forest.—We recorded 324 bird species representing 45 families in *terra firme* forest on both sides of the river, and detected 155 species only in this habitat. Thamnophilidae (43 species) and Tyrannidae (42 species) were the most diverse families.

TABLE 3. Species within which we detected multiple diagnosable forms in the study area.

Genus/species	Hypothetical taxon 1	Hypothetical taxon 2	Hypothetical barrier
<i>Himantopus mexicanus</i>	<i>mexicanus</i>	<i>melanurus</i>	? ^a
<i>Phaethornis malaris</i>	<i>moorei</i>	“ <i>ucayalii</i> ” ^b	Ucayali River
<i>Capito auratus</i>	<i>punctatus</i>	<i>insperatus</i>	Ucayali River
<i>Myrmoborus leucophrys</i>	<i>koenigorum</i> ^c	<i>leucophrys</i>	? ^a
<i>Willisornis poecilinotus</i>	<i>lepidonotus</i>	<i>griseiventris</i>	Ucayali River
<i>Dendrocincla fuliginosa</i>	<i>phaeochroa</i>	<i>atirostris</i>	Ucayali River
<i>Dendrocolaptes certhia</i>	<i>radiolatus</i>	<i>juruanus</i>	Somewhere on west bank of Ucayali River
<i>Philydor erythrocerum</i>	<i>lyra</i>	<i>ochrogaster</i>	Ucayali River
<i>Lepidothrix coronata</i>	<i>exquisita</i>	<i>coronata</i> ^d	Ucayali River
<i>Schiffornis turdina</i>	<i>steinbachi</i>	<i>amazona</i>	Ucayali River
<i>Microcerculus marginatus</i> ^e	<i>marginatus</i> (N voice type)	<i>marginatus</i> (S voice type)	Ucayali River

^a Presence of intermediates complicates determination of a barrier.

^b This taxon (Zimmer 1950) may represent intergrades between *P. m. moorei* and *P. m. bolivianus* (Hinkelmann 1996).

^c *M. l. koenigorum* is described from the Huallaga Valley (O’Neill and Parker 1997), but individuals in the Sira resemble this form in plumage and are generally distinguishable from lowland populations.

^d Individuals appear intermediate between *L. c. coronata* and a green-bodied form (presumably *L. c. exquisita* or *L. c. caelestipileata*).

^e Although treated as the same subspecies, vocal differences between these populations are well known (e.g. Ridgely and Tudor 1989).

Birds of Floodplain Forest.—We recorded 237 bird species representing 40 families in *várzea*- and *igapó*-like floodplain forests, and detected 36 species only in these habitats. Thamnophilidae (30 species) and Tyrannidae (28 species) were the most diverse families. One-hundred and forty-six species were shared between *terra firme* and floodplain forest.

Birds of Successional Habitats.—We recorded 129 bird species representing 34 families in open and successional habitats. Tyrannidae (27 species) and Thraupidae (16 species) were the most diverse families. Many of the species recorded in this habitat are widespread in open areas in the Amazon Basin, but we also recorded some species that are rare and local in Amazonia, including Barn (*Tyto alba*) and Burrowing (*Athene cucularia*) owls and Pearl Kite (*Gampsonyx swainsonii*). Migrants were numerous in this habitat; we recorded nine boreal and 15 austral migrant species, including rare migrants (Schulenberg et al. 2010) such as Slaty Elaenia (*Elaenia strepera*) and Plain Tyrannulet (*Inezia inornata*).

Birds of Stunted Forest.—We recorded 45 bird species representing 20 families in stunted forest, and detected eight species (and one subspecies) only in this habitat. Tyrannidae (nine species), Thamnophilidae (four species), and Furnariidae (four species) were the most diverse families. In the most stunted sections of forest (1–10 m canopy height), birds were scarce. Scissor-tailed Nightjar (*Hydropsalis torquata*), Rufous-throated Sapphire (*Hylocharis cyanus*), Zimmer’s Tody-Tyrant

(*Hemitriccus minimus*), one subspecies of Fuscous Flycatcher (*Cnemotriccus fuscatus duidae*), Brown-crested Flycatcher (*Myiarchus tyrannulus*), and Black Manakin (*Xenopipo atronitens*) were found only within this habitat. A few birds reached higher density in this habitat than elsewhere, including Scaled Pigeon (*Patagioenas fasciata*), White-flanked Antwren (*Myrmotherula axillaris*), Cinnamon Neopipo (*Neopipo cinnamomeus*), and Epaulet Oriole (*Icterus cayanensis*). Five presumed migrant species were recorded in the stunted forest, although it is possible some of these, such as *Hydropsalis torquata* and *Myiarchus tyrannulus*, breed locally. In forest of moderate canopy height fringing the stunted forest, Brazilian Tinamou (*Crypturellus strigulosus*), Brown-banded Puffbird (*Notharchus ordii*), Paradise Jacamar (*Galbula dea*), Bar-bellied Woodcreeper (*Hylexetastes stresemanni*), Lineated Woodcreeper (*Lepidocolaptes albolineatus*), Rufous-winged Foliage-Gleaner (*Philydor erythropterum*), Slender-billed Xenops (*Microxenops milleri*), Yellow-browed Antbird (*Hypocnemis hypoxantha*), Rufous-tailed Flatbill (*Ramphotrigon ruficauda*), Citron-bellied Attila (*Attila citriniventris*), Thrush-like Schiffornis (*Schiffornis turdinus*), Yellow-backed Tanager (*Hemithraupis flavicollis*), and Short-billed Honeycreeper (*Cyanerpes nitidus*) reached their highest local densities. Silky-tailed Nightjar (*Caprimulgus sericocaudatus*) was only recorded here. In isolated open palm swamps (*aguajales*) within the stunted forest, the two palm swamp specialists Point-tailed Palmcreeper (*Berlepschia rikeri*) and Sulphury Flycatcher

(*Tyrannopsis sulphurea*) were common, as were Smooth-billed Ani (*Crotophaga ani*), Swallow-winged Puffbird (*Chelidoptera tenebrosa*), and Palm Tanager (*Thraupis palmarum*), species typical of disturbed or riverine habitats and not generally found in *terra firme*.

Birds of Bamboo Patches.—We recorded 10 bird species representing five families in the bamboo, and detected six species only in this habitat. Thamnophilidae (three species) and Tyrannidae (three species) were the most diverse families. Birds known to specialize on bamboo (Kratzer 1997) that we observed in this habitat were Rufous-breasted Piculet (*Picumnus rufiventris*), Dusky-cheeked Foliage-Gleaner (*Anabazehops dorsalis*), Red-billed Scythebill (*Campylorhamphus trochilirostris*), Dot-winged Antwren (*Microrhopias quixensis*), Striated Antbird (*Drymophila devillei*), Manu Antbird (*Cercomacra manu*), Large-headed Flatbill (*Ramphotrigon megacephalum*), Dusky-tailed Flatbill (*R. fuscicauda*), and White-cheeked Tody-Flycatcher (*Poecilatriccus albifacies*). We also observed the *obscurus* subspecies of Long-billed Gnatwren (*Ramphocaenus melanurus obscurus*) primarily in or adjacent to bamboo. In addition, the Olallas collected White-lined Antbird (*Pernostola lophotes*), a species often associated with bamboo (Kratzer 1997), in the region in 1928 (Appendix II).

Birds of River Islands.—We recorded 37 bird species representing 12 families on islands in the Ucayali and lower Tambo rivers, and detected 13 species (and one subspecies) only in this habitat. Tyrannidae (11 species) and Thraupidae (six species) were the most diverse families. Species restricted to this habitat in the region, many of which have been classified as river island specialists (Rosenberg 1990), included Black-banded Crake (*Anurolimnas fasciatus*), Festive Parrot (*Amazona festiva*), Lesser Hornero (*Furnarius minor*), White-bellied (*Synallaxis propinqua*) and Parker's (*Cranioleuca vulpecula*) spinetails, Castelnau's Antshrike (*Thamnophilus cryptoleucus*), Black-and-white Antbird (*Myrmochanes hypoleucus*), Spotted Tody-Flycatcher (*Todirostrum maculatum*), River Tyrannulet (*Serpophaga hypoleuca*), Lesser Wagtail-Tyrant (*Stigmatura napensis*), Spotted Tody-Flycatcher (*Todirostrum maculatum*), one subspecies of Fuscous Flycatcher (*Cnemotriccus fuscatus fuscator*), and Riverside Tyrant (*Knipolegus orenocensis*).

Olive-spotted Hummingbird (*Leucippus chlorocercus*) was most common on river islands, but was also observed once in successional habitat near Atalaya, and several times in flight between islands and the shoreline.

Range Extensions and Vagrants

We recorded 22 species well outside of their known ranges (Schulenberg et al. 2006b, 2010). These records represent either range extensions for species that are likely resident in the region, or records of presumed wandering individuals from elsewhere. Below, we provide brief accounts for these species and biogeographic context based on a review of prior records:

Black-bellied Whistling-Duck (*Dendrocygna autumnalis*).—A single individual was observed at Otorongo by MGH flying overhead at dawn on 7 June 2011, and three individuals were observed by GFS and RST flying low over Atalaya at dusk on 7 July 2011. This species is rare in Peru, and primarily known from the Pacaya-Samiria region to the north. These are the first records from Ucayali Region.

Brazilian Teal (*Amazonetta brasiliensis*).—A pair was observed by MGH at close range on 7 May 2011 on the river island at the mouth of the Tambo River. They were not relocated on subsequent visits to the site. This species is presumably a very rare austral migrant to Peru, with few prior records, all from Madre de Dios Region. It appears to have become increasingly common, however, in recent years (MGH, pers. obs.; T. Schulenberg pers. comm.).

Puna Ibis (*Plegadis ridgwayi*).—DCA, MGH, SFR, and FHC observed a flock of four individuals flying over an open field bordering Quebrada Yanayacu along the track between Carachao and Chorinashi (10° 35' S, 73° 78' W; 290 m). The birds circled low overhead before flying southeast. This species is restricted to high altitude wetlands in the Andes and is a rare vagrant to the western Amazon Basin. This is the first record for Ucayali Region.

Black-faced Hawk (*Leucopternis melanops*).—An individual was observed on 6 January 2008 at the edge of a pasture outside of Atalaya (BMW, GFS, MGH). *L. melanops* is typically a species of northern Amazonia, where it was thought to replace the similar White-browed Hawk (*L. kuhli*), but it has recently been detected in a number of localities in the southwestern and south-central Amazon (Barlow et al. 2002, Raposo do Amaral et al. 2007, Shrum et al.

2011). In many of these locations, including in our study area, *L. melanops* and *L. kuhli* appear to be present in sympatry. This is the first record of *L. melanops* from Ucayali Region.

Burrowing Owl (*Athene cunicularia*).—Burrowing Owls were observed on at least three occasions in fields around the town of Atalaya and on river islands in the Tambo River and Ucayali River. Two agitated adults and two downy young barely capable of flight were observed on 17 October 2008 in a field southeast of Atalaya (MGH). Two adults, including a female with a calcified egg in the oviduct, were collected on an island in the Tambo River on 24 July 2010 (LAAL, GB, MGH, FHC). Formerly unknown from the Peruvian Amazon, this species has recently been found in small numbers in agricultural areas and along rivers in Loreto and Madre de Dios Regions. These records constitute the first for Ucayali Region and the first documented breeding observations from the Peruvian Amazon.

Fiery Topaz (*Topaza pyra*).—This species was first detected in the study area at Canuja 20–22 July 2010. At least three males and one female were observed feeding and interacting over a rocky stream in foothills at 450 m, and two males were collected. At least two males were observed and one male was collected at Carachao 24–29 May 2011. Here, they occurred in *aguajales* within terra firme forest. *Topaza pyra* was previously known in Peru only from Loreto Region in the northeast. The closest prior record, and the previous southernmost record for the species, comes from the Sierra del Divisor 350 km to the north (Schulenberg et al. 2006a).

Rufous-throated Sapphire (*Hylocharis sapphirina*).—One individual was netted and collected at the Cohengua Stunted Forest on 12 June 2011. This is the first record of this species from south of the Amazon River and east of the Ucayali River in Peru.

Brown-banded Puffbird (*Notharchus ordii*).—This species was fairly common at Otorongo and in the Cohengua Stunted Forest 2–13 June 2011. It occurred chiefly in taller stunted forest, but was present in tall *terra firme* forest as well. We obtained audio recordings and four specimens. This species is patchily distributed in Peru, often in areas with nutrient poor soils. This is the first record from Ucayali, with the closest prior record in the Sierra del Divisor 350 km to the north (Schulenberg et al. 2006a). These records bridge a gap in the distribution of *N. ordii* between the

varillales of Loreto Region and a few isolated records in Madre de Dios Region.

Spotted Puffbird (*Bucco tamatia*).—Two individuals (a male and female) were netted and collected in *terra firme* forest at Otorongo on 2 June 2011. This species was previously known in Peru only from Loreto Region and an isolated record in Madre de Dios Region. This is the first record from Ucayali Region.

Short-billed Leaf-tosser (*Sclerurus rufularis*).—Two individuals were collected in *terra firme* forest at Otorongo on 6 and 10 June 2011. This species was previously known in Peru only from Loreto Region. These constitute the first records for Ucayali Region and a range extension of 300 km to the south.

Fulvous Antshrike (*Frederickena fulva*).—A single male was observed and recorded by JGT on 27 August 2009 in dense understory of *terra firme* forest at ~300 m at Tambo on the west side of the Ucayali River. The recorded loudsong of this individual was consistent with *F. fulva* and distinct from the Undulated Antshrike (*F. unduliger*) recorded by GFS at Otorongo on the east side of the Ucayali River. This record extends the distribution of *F. fulva* 290 km south-southeast from the Rio Cushabatay, Loreto Region (Isler et al. 2009).

Black Bushbird (*Neotantes niger*).—This species was uncommon in edge habitats at Carachao and Otorongo 27 May–15 June 2011. We obtained audio recordings and four specimens, including one female specimen with associated recordings. This is the first record from Ucayali Region and bridges a gap in the distribution of *N. niger* between Loreto and Madre de Dios Regions.

Zimmer's Tody-Tyrant (*Hemitriccus minimus*).—This species was fairly common in stunted forest of 8–15 m canopy height in the Cohengua Stunted Forest. We obtained audio recordings of songs and calls of several individuals. These are the first records for Ucayali Region and represent a range extension of 400 km from the nearest localities in Loreto Region.

Yellow-throated Spadebill (*Platyrinchus flavigularis*).—A single individual was observed and recorded by JGT on 28 August 2009 on a ridge at ~450 m near Tambo. The vegetation in this area is transitional between *terra firme* forest and montane evergreen forest. This species is known from few localities on the east slope of the Peruvian Andes and outlying ridges from 1,200–2,000 m (Schulenberg et al. 2006b, 2010), but this record constitutes the first record for Ucayali Region, the

first record for the Sira Range, and a downward elevational range extension of ~750 m.

Cinnamon Neopipo (*Neopipo cinnamomea*).—This species was first detected in the study area when one was netted and collected in foothill forest at 300 m at Canuja on 20 July 2010. Between 30 May–14 June 2011, we found it to be rare in *terra firme* forest at Otorongo and fairly common at the Cohengua Stunted Forest, where one individual was recorded and collected. This species is local in much of its range. The closest generally accepted records are from Huánuco and Madre de Dios Regions, although the Olallas collected a specimen from Santa Rosa (near Atalaya) in 1927.

Fuscous Flycatcher (*Cnemotriccus fuscatus*).—At least two subspecies were recorded in the region. *Cnemotriccus f. fuscator* was commonly recorded on river islands in the Ucayali and Tambo rivers 16–19 October 2008, 24 July 2010, and 7 May–2 July 2011. We obtained eight specimens of this subspecies. *C. f. duidae* was fairly common at the Stunted Forest 11–14 June 2011, and we obtained audio recordings and five specimens. These are the first records of *C. f. duidae* from Ucayali Region. The nearest previous records are from the Sierra del Divisor in southern Loreto Region (Schulenberg et al. 2006a). These two taxa are widely sympatric (here within 36 km of each other), occur in different habitats, and have different vocalizations, and thus should be treated as separate species.

Riverside Tyrant (*Knipolegus orenocensis*).—This species was first observed and recorded 16–17 October 2008 (DCA, MGH, GFS, BMW), when up to five individuals were present on an island at the mouth of the Tambo River. MGH recorded and collected a displaying male and observed a female just upriver in Junín Region on 24 July 2010. Five individuals were netted and collected on the island in the mouth of the Tambo River on 6 July 2011. This species is known in Peru only from along the Amazon and lower Marañón rivers in Loreto Region. These are the first records from Ucayali and Junín Regions and constitute a range extension of 600 km.

Yellow-throated Flycatcher (*Conopias parvus*).—This species was fairly common at Otorongo and the Cohengua Stunted Forest and uncommon at Carachao between 29 May–15 June 2011. We obtained audio recordings and five specimens. This species is known in Peru from Loreto Region, particularly in areas with nutrient

poor soils. These are the first records for Ucayali Region.

Crested Becard (*Pachyramphus validus*).—One female was collected at Otorongo on 15 June 2011 (RST). This species is resident along the eastern slopes of the Andes (*P. v. audax*) and an austral migrant to southeastern-most Peru (*P. v. validus*). Although not identified to subspecies, this individual was likely of the migrant form, and represents a first record for Ucayali Region.

Citron-bellied Attila (*Attila citriniventris*).—This species was fairly common at Otorongo and the Cohengua Stunted Forest and uncommon at Carachao between 25 May–15 June 2011. We obtained audio recordings and three specimens. This species is known in Peru only from Loreto Region, particularly in areas with nutrient-poor soils. These are the first records for Ucayali Region and constitute a range extension of 450 km.

Black Manakin (*Xenopipo atronitens*).—We found this species to be fairly common in short scrub <5 m in stature at the Cohengua Stunted Forest. We obtained audio recordings and collected four individuals. This species is patchily distributed in *varillales* throughout the Amazon Basin, but in Peru is known only from Jeberos in Loreto Region and Pampas del Heath in Madre de Dios Region. These are the first records for Ucayali Region.

Green Oropendola (*Psarocolius viridis*).—One individual was observed by BMW and MGH at Misión Unine on 8 January 2008, and three individuals were collected, two by LAAL and one by WAGB, at Quebrada Sipiria between 11–31 August 2009. Prior records from central Peru are few, but these additional records at different times of year suggest the presence of a population rather than isolated wanderers.

DISCUSSION

Our results represent the first inventory of the upper Ucayali River aside from the work of the Olalla brothers in 1927–1928. With the addition of 30 species that they recorded but were not recorded during our work (online Supplemental Material), the bird list for the upper Ucayali River would total 594 species. Locality information associated with the Olalla specimens has been questioned in the past, but recent re-examination of their specimens suggests that erroneous data can be isolated to a few portions of their collections (Wiley 2010). Specimens acquired by AMNH with the collections of Harvey Bassler, for example, are labeled

erroneously (and are not included in the online Supplemental Material). Specimens collected by Alfonso Olalla in March 1928 were labeled with the locality “Lagarto” from the right bank, but no location report was sent for this period and it is possible he was collecting on both banks. This possibility is supported by the presence in this collection of several species that we found only on the left bank (online Supplemental Material). Overall, however, there are few discrepancies between our results and the Olalla specimens. Our results support the assertion (Wiley 2010) that the Olalla data, with the exceptions mentioned above, are largely accurate.

The results of our inventory work, combined with prior information on bird distributions in nearby areas, suggest that the upper Ucayali River is a less effective barrier to species distributions than is the middle Ucayali River. This pattern is likely because of the greater ease with which birds might move across the narrow upper Ucayali River and its tributaries relative to the wider middle Ucayali River. Passive transport, the transfer of land and organisms from one side of the river to the other because of changes in the course of the river, may also play a role. The Ucayali has a history of frequent shifts within its alluvial plain, particularly along the lower stretches in the Pacaya-Samiria region (Lathrap 1968, Dumont 1991). These shifts may have been responsible for the movement of animal populations across the lower Ucayali River (Tuomisto and Ruokolainen 1997), and similar passive transfers may be responsible for the occurrence of some bird species on the “wrong” side of the upper Ucayali River.

With the decreased efficacy of the upper Ucayali as a barrier comes the potential for contact, hybridization, and introgression between geographic replacements. We found 20 pairs of taxa with largely allopatric or parapatric distributions in close proximity in the region of the upper Ucayali River, and possible intergrades or hybrids between three of those taxon pairs. It is likely both of these numbers are conservative estimates. We were only able to detect divergent forms for taxa from which we had sufficiently large samples (of observations, recordings, or specimens). Many of the taxa that potentially come into contact here are cryptic and difficult to separate, even in the hand. In addition, our sampling did not extend above the confluence of the Ucayali River with the Tambo and Urubamba rivers, where the potential for observing intergradation may be even higher. Genetic work also

promises to provide a clearer picture of the number of contact zones and the extent of introgression between closely related taxa in this region. Recent work in other headwaters regions has begun to uncover instances of interbreeding between geographic replacements (Naka et al. 2012). It seems likely that, as more work is done in Amazonian headwaters, more zones of contact and cases of introgression and hybridization will be discovered.

The upper Ucayali River lies at the confluence of major Amazonian avifaunas. Parker et al. (1996) divided the Amazon into northern and southern regions, and we found that the avifauna of the upper Ucayali River shares affinities with both. Cracraft (1985) further divided the Amazon into smaller areas of endemism, and the upper Ucayali River lies near the confluence of two such areas - the Napo and Inambari. The delineation of the northern and southern Amazon, as well as the Napo and Inambari areas of endemism, is complicated, however, by the biogeographic complexity of the upper Ucayali River and nearby regions in the northern and central Peruvian Amazon. Although the boundary between areas is often ascribed to the Marañon River in northern Peru, many distributional limits in the region occur elsewhere, including at the Ucayali River, the Pachitea River, the Cordillera Azul, the Huallaga River, and in some cases in areas with no obvious landscape feature to serve as a barrier (Schulenberg et al. 2006b, 2010). The disparity in the locations of distributional limits is likely because of the absence of a single major barrier in this region, and is consistent with observed patterns in distributional limits between taxa and phylogeographic groups in other headwaters regions (Bates et al. 2004, Naka et al. 2012). The presence and positions of distributional limits in northern and central Peru have likely been determined by the cumulative effects of many landscape features, perhaps in conjunction with the effects of competition with Andean taxa (Terborgh and Weske 1975) or historical effects resulting from forest retraction (Haffer 1969), shifts in river courses (Sick 1967), downward influxes of montane habitats (Bush 1994), or the dynamic nature of the history of range expansion, contraction, and local extinction of each species (Brumfield 2012).

The avian diversity of the upper Ucayali River is likely at least partly attributable to the high diversity of habitats in the region. Many Amazonian habitats important to birds are present in the

region, including some with restricted distributions, such as stunted forest, bamboo, and river islands. These habitats both contribute to overall diversity, and provide important habitat for specialists, some of which are of conservation concern.

Successional habitats are of particular interest in the upper Ucayali Valley because they have been heavily influenced by human activity. Open areas have likely increased as a result of colonization and human expansion, and this trend may be driving the appearance of a number of species described above that have been considered rare or local in the Amazon Basin. Burrowing Owl in particular may be a recent colonist of the Peruvian Amazon, but other species may soon follow. Successional areas are important not only to residents arriving from elsewhere, but also to boreal and austral migrants. We recorded a high diversity of migrants in successional and edge habitats, and it seems likely these species will be influenced, as well as forest interior species, as deforestation continues.

The extraction of timber, petroleum, and gold, as well as deforestation for human habitation and farming, threaten the forests and other habitats of the upper Ucayali River. Conflict between indigenous groups, colonists, and corporations creates a difficult environment for conservation efforts regionally. The upper Ucayali warrants conservation not only for its avian diversity, but also for its biogeographic complexity and potential as a natural laboratory for evolutionary research.

ACKNOWLEDGMENTS

We thank the Ashéninka communities of the Organización Indígena Regional de Atalaya and Asociación Regional de Pueblos Indígenas, the Ashéninka community of La Selva, and the Shinipo-Conibo community of Amaquiria for their support. We thank especially our local guides for their committed assistance and protection. The Consorcio Forestal Amazónico provided access and logistical support. We are very grateful to R. H. and M. Wiley for sharing their carefully collected data on the Olalla specimens at the American Museum of Natural History. G. F. Budney (ML) and D. L. Dittmann and S. W. Cardiff (LSUMNS) were generous in support of logistical aspects of the collecting and recording efforts. I. J. Lovette, J. W. Fitzpatrick, J. P. O'Neill, and D. W. Winkler provided encouragement early during the project. M. J. Miller provided helpful unpublished data on bird distributions. T. S. Schulenberg, D. F. Lane, and M. L. Isler gave generously of their extensive knowledge of the Peruvian avifauna. J. V. Remsen, R. T. Brumfield, T. H. Valqui, J. M. Bates, and J. L. Cracraft provided financial, logistical,

and intellectual support throughout. M. L. Isler, M. B. Robbins, R. H. Wiley, J. V. Remsen, and R. T. Brumfield provided helpful comments on the manuscript. We thank the Dirección General Forestal y de Fauna Silvestre (DGFFS) of Peru for permission to collect in the region (Reserva Comunal El Sira N° 001-2009, RD N°0345-2010, RD N°0281-2011). Thanks to D. Mishari, Chief of the Reserva Comunal El Sira, for facilitating permission to work within the Reserve. Funding and support for fieldwork were provided by the National Geographic Society, Cornell Laboratory of Ornithology, National Science Foundation (grant DEB-0841729 to Robb T. Brumfield), Explorer's Club, Cornell Presidential Research Scholars, Jordani Zoology Club, Eastern Mountain Sports, H. B. Conover Fund and the Ornithological Research Fund of the Field Museum's Bird Division, and the American Museum's F.M. Chapman Memorial and L. J. and L. C. Sanford Funds.

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