

AVIAN BIOGEOGRAPHY OF AMAZONIAN FLOODED FORESTS IN THE RIO BRANCO BASIN, BRAZIL

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ABSTRACT.—Flooded forests represent an important part of Amazonian diversity, yet the distribution, ecology, and evolutionary history of the avifauna of these forests have received little attention. We conducted ornithological surveys in the Rio Branco Basin, which is entirely in the Brazilian State of Roraima. In this paper, we discuss the presence of 20 bird species recorded along the lower Rio Branco, 16 of which represent new records for the State of Roraima and the entire Rio Branco Basin. Among our most interesting records are four species of white-water river specialists (*Synallaxis propinqua*, *Stigmatura napensis*, *Serpophaga hypoleuca*, and *Conirostrum bicolor*) that have populations on the lower Rio Branco, isolated from other Amazonian white-water river systems by the black waters of the Rio Negro where they do not occur. We also discovered new localities for the endemic and endangered Rio Branco Antbird (*Cercomacra carbonaria*), doubling the size of its known range. We discuss the implications of these records in a biogeographic perspective for better understanding the distributional patterns of the flooded-forest avifauna in Amazonia. Received 11 May 2006. Accepted 12 December 2006.

The Amazon Basin contains the most spectacular river system on earth. Not only is the Amazon River the longest and largest river in the world, but some of its tributaries also rate among the 10 largest (Goulding et al. 2003). These rivers create the Amazonian flood plains, a mosaic of habitats which remain flooded for as much as 8 months every year (Junk 1989). These seasonally flooded habitats, known in Brazil as *várzeas* and *igapós*, include floating meadows, sandbar scrub, river-edge forest, and tall flooded forest each hosting a diverse and highly specialized avifauna that accounts for at least 15% of Amazonia's overall non-aquatic bird diversity (Remsen and Parker 1983).

Despite the continental extent of this ecosystem, which ranges thousands of kilometers across northern South America, from the base of the Andes to the Atlantic Ocean, the distribution, ecology, and evolutionary history of its avifauna have been poorly studied. Until

recently, flooded forests have not captured the attention of avian biogeographers (Cohn-Haft et al. in press), who have focused mostly on describing bird distribution patterns and generating evolutionary hypotheses for Amazonian *terra firme* forests (e.g., Sick 1967, Haffer 1969, Norens 1999). We attribute this lack of interest in the biogeography of flooded forest birds, in part, to the general assumption that these birds, by living in dynamic and relatively ephemeral habitats, must have strong dispersal abilities. Strong dispersal abilities in continuous, linear environments should not favor genetic isolation and differentiation of populations, leading to the expectation of widespread species with little or no geographic variation (Remsen and Parker 1983). The lack of precise distributional data for *várzea* birds has also prevented ornithologists from making historical interpretations that go beyond a handful of species (e.g., Haffer and Fitzpatrick 1985, Haffer 1997, Isler et al. 1999, Aleixo 2006).

The Rio Branco is unique in Amazonia, because it is a nutrient-rich, semi-muddy river, surrounded by black-water rivers (poor in sediments and nutrients, but rich in organic matter). The 'color' of the water has important ecological implications, because muddy and semi-muddy rivers (hereafter 'white-water' rivers) differ from black-water rivers not only in the amount of sediments they carry, but also in the structure and composition of the

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vegetation along their margins (Klinge and Furch 1991), affecting the species richness and composition of its associated avifauna (Rosenberg 1990, Petermann 1997, Borges and Carvalhaes 2000). Many widespread flooded-forest birds occur in riverine habitats created by both types of rivers, but some are restricted to either black-water or white-water rivers. White-water river specialists that are present on the Rio Branco are necessarily isolated from other white-water drainages of Amazonia, potentially allowing genetic and population differentiation.

The Rio Branco Basin lies in a region of high habitat heterogeneity and of great ecological and biogeographical interest, important for our understanding of distributional patterns of Amazonian birds (Naka et al. 2006). The only major ornithological explorations on the Rio Branco until the mid 20th century were those of Natterer in 1831 and 1832 (von Pelzeln 1868–1871). More recently, Stotz (1997) and Zimmer et al. (1997) surveyed the river, but like Natterer only explored the upper Rio Branco, where river-created habitats consist of narrow stretches of gallery forest. The avifaunas of gallery and flooded forests are generally distinct; the former being more closely related to dry forests in the savannas than to Amazonian flooded forests. The first comments on the birds of the lower Rio Branco were published by Pacheco (1995) after a short visit to the mouth of the river and by Santos (2004), who worked on several river islands near Caracaraí.

This paper reports our most interesting observations obtained during several avifaunal surveys on the lower Rio Branco since 1990, including several significant range extensions and 16 species new to the Rio Branco Basin and the State of Roraima. We discuss the biogeographical implications of these records and call attention to the presence of previously overlooked and possibly isolated populations of white-water river specialists on the Rio Branco.

METHODS

Study Area.—The Rio Branco Basin is within the Brazilian State of Roraima (Fig. 1) and the river is the largest tributary of the Rio Negro, itself the second-largest tributary of the Amazon and the largest black-water river

in the world. The basins of the Rio Negro and Rio Branco jointly contribute nearly 15% of the total annual discharge of the Amazon River and occupy an area of roughly 700,000 km², more than 10% of the Amazon Basin (Goulding et al. 2003). The Rio Branco is not as turbid as the Amazon or the Madeira rivers, but its waters contrast strongly with the dark waters of the Negro. On satellite imagery, this “meeting of the waters” can be seen for more than 50 km downstream from their confluence.

We divide the Rio Branco in two main geographical and ecological regions: the upper and lower Rio Branco with the city of Caracaraí (01° 50' N) as the dividing point. About 70 km north of Caracaraí, coinciding with the confluence of the Rio Branco and the Rio Mucajaí, rainfall decreases sharply (Barbosa 1997) and soil conditions change drastically (Brown and Prance 1987). Savannas replace lowland Amazonian forests in this region and, along the rivers, gallery forests replace flooded forests. We have not sampled the Rio Branco between Caracaraí and Mucajaí, and do not know how gradually these changes occur. However, apparently many flooded-forest bird species readily found around Caracaraí are not present in the gallery forests of the Rio Mucajaí or Rio Branco from Mucajaí north.

The terms *várzea* and *igapó* are local terms used to describe flooded forests and are often used interchangeably by local inhabitants. Here, we follow Prance (1979) using these terms to distinguish forests based on the kind of water that floods them: *várzea* for forests flooded by white (muddy) waters and *igapó* for forests flooded by black (translucent, acidic) waters. The banks of the lower Rio Branco are covered by extensive *várzeas*, whereas many of its tributaries (i.e., Água Boa do Univini, Iruá, and Ajarani) are black-water rivers, whose margins are covered by *igapó*.

The Rio Branco has an average river-level fluctuation of 5.7 m, which is enough to flood large areas along the river, and to ‘dam’ smaller tributaries (Goulding et al. 2003). Vegetation structure and floristic composition depend on the duration and level of the flooding; areas flooded for longer periods tend to support fewer tree species (Junk 1989). The *várzeas* of the Rio Branco have a well-developed canopy reaching 20–25 m in height, and the un-

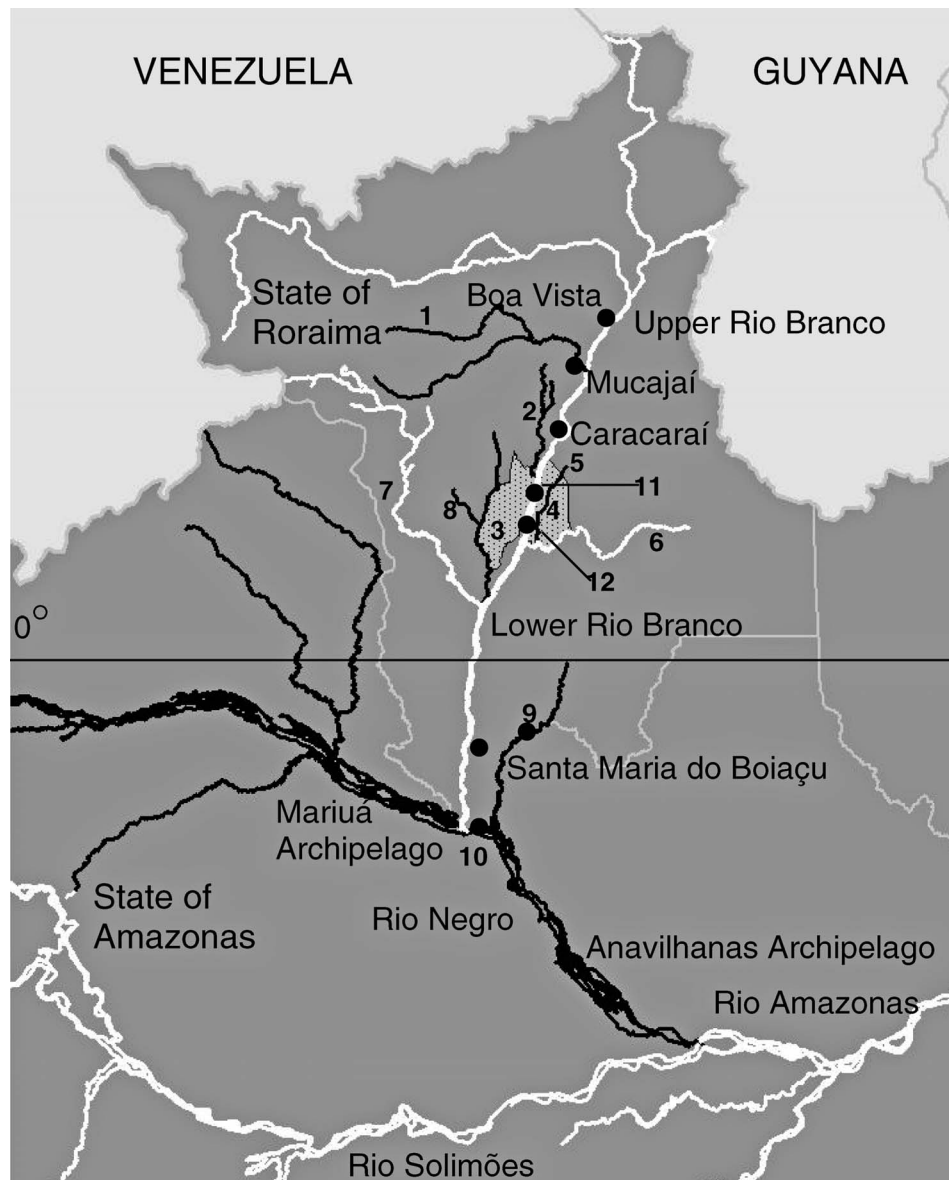


FIG. 1. The Rio Branco Basin and study localities, enclosed by the Brazilian State of Roraima, and included within the Rio Negro Basin. White-water rivers are white; black-water rivers are black. Stippled areas represent reserves. Numbers represent the following rivers or localities: (1) Rio Mucajaí, (2) Rio Ajaraní, (3) Niquiá Ecological Station, (4) Viruá National Park, (5) Rio Iruá, (6) Rio Anauá, (7) Rio Catrimani, (8) Rio Água Boa do Univini, (9) village of Samaúma on the Rio Jauaperí, (10) Paraná da Floresta, (11) Marari Island, and (12) Inajatuba island. Digital data obtained from Ministério do Meio Ambiente (2001).

derstory is generally open and poorly developed. Tree species diversity and complexity of vertical structure on river islands increase as an island ages (Robinson and Terborgh 1997) creating a series of successional stages that

range from sandbars to river-edge forest (dominated by *Cecropia*) to mature *várzea* forest, which has the highest number of tree species (Remsen and Parker 1983). *Igapós* are usually associated with sandy soils and have

fewer tree species than *várzea* forests, narrower tree diameters, and a lower canopy height (15–20 m). The physiognomy and floristic composition of the *igapó* resemble that of white-sand forests (Anderson 1981).

Field Work.—AW visited the lower Rio Branco near the mouth of the river on 10–11 June and 22–24 December 1990, 6–7 April 1991, 19–20 August 1993, 25–26 January and 25–26 July 1994, 24–25 March and 15–16 July 1995, and 9–10 June 1996. MCH made a short visit to the mouth of the Rio Branco on 6 July 1999. In 2001 and 2006 we joined three expeditions sponsored by the *Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis* (IBAMA) to survey the avifauna of the lower Rio Branco and some of its tributaries. Between 6 and 11 July 2001, LNN and MFT covered ~100 km of the Rio Branco (from Santa Maria do Boiaçu to the mouth of the river), a short stretch of the Rio Negro influenced by the Rio Branco (Paraná da Floresta), and the west bank of the Rio Jauaperí (from its mouth to the village of Samaúma). Between 5 and 18 October 2001, LNN and JMB covered ~170 km of the Rio Branco from Caracaraí south to the mouth of the Rio Catrimani and some Rio Branco tributaries (Água Boa do Univini, Iruá, Anauá, and Ajarani rivers). Between 1 and 15 October 2006, LNN and MCH, accompanied by Marcelo dos Santos Jr. and Catherine L. Bechtoldt, studied ~80 km of the Rio Branco from Caracaraí to the confluence with the Rio Anauá, and another 35 km up the white-waters of the Rio Anauá and a similar distance along the black-waters of the Rio Iruá.

We usually conducted bird surveys during early morning (0500–1200 hrs), late afternoon (1500–1830 hrs), and sporadically at night using binoculars and tape-recorders. We explored river-created habitats (*várzea* and *igapó*) using small motorboats, which allowed access to the forest interior. LNN and MCH collected bird specimens, housed at the *Instituto Nacional de Pesquisas da Amazônia* (INPA) Bird Collection in Manaus, Brazil. Tape-recordings by LNN and MCH are archived at the INPA Bird Collection; those by AW are at the British Library National Sound Archive. Taxonomy and species nomenclature follow the Brazilian Ornithological Records

Committee (Comitê Brasileiro de Registros Ornitológicos 2006).

RESULTS

We present details of 20 species recorded during our fieldwork which represent either new records for the Rio Branco Basin and the State of Roraima (species marked with an asterisk), or note-worthy range extensions.

Species Accounts

**Leucopternis schistaceus* (Slate-colored Hawk).—AW found two single individuals on river islands on the lower Rio Branco (15 and 27 km north of the river's mouth) on 10 June 1990 and 7 April 1991, respectively. In October 2001 LNN and JMB observed and tape-recorded two birds in tall *várzea* forest along the east bank of the lower Rio Branco (01° 36' 20" N, 61° 13' 08" W) at Viruá National Park. This species seems to be restricted to tall flooded forests in Brazil (Bierregaard 1994) and probably occurs in the State of Roraima only along the lower Rio Branco.

**Asio stygius* (Stygian Owl).—AW observed one bird perched on a sand bar of a river island 25 km north of the mouth of the Rio Branco on the night of 22 December 1990. In subsequent visits to that island the following day and following year (April 1991) AW repeatedly found an individual there (presumably the same bird). This species is widely distributed from Mexico to Argentina, but seems to be rare and local (Marks et al. 1999). This owl generally inhabits savannas in Amazonian Brazil, but in recent years AW has obtained several records from areas associated with black-water rivers and river islands.

**Monasa nigrifrons* (Black-fronted Nunbird).—AW found this species along the lower Rio Branco on 23 December 1990 and in successive trips to the same general area. Subsequently, LNN, JMB, and MFT observed and tape-recorded several individuals in *várzea* forest along both banks of the lower Rio Branco. Our records ranged from the mouth of the river north to the island of Inajatuba (01° 17' 22" N, 61° 18' 04" W), nearly 60 km south of Caracaraí. This species is widespread in Amazonia, mostly restricted to flooded forests (Rasmussen and Collar 2002), but seems to be restricted in the State of Roraima to the *várzeas* of the lower Rio Branco, with no known

records from gallery forests further north or from Venezuela (Hilty 2003).

**Myrmotherula klagesi* (Klages' Antwren).—AW heard and observed several pairs in mature *várzea* forest ~20 km north of the mouth of the Rio Branco on 23 December 1990. Birds were subsequently tape-recorded by AW along both banks of the Rio Jauaperí in August 1993 and other sites along the lower Rio Branco in June 1993 and July 1995. MCH tape-recorded the species near the mouth of the Rio Branco in July 1999, and in July and October 2001, LNN and MFT, and LNN and JMB, respectively, documented its presence throughout the lower Rio Branco, obtaining tape-recordings from the mouth of the river as far north as the island of Inajatuba, 300 km to the north. On 6 October 2006 MCH tape-recorded and collected a male from a river island on the Rio Branco, opposite the mouth of the Rio Anauá, representing the first specimen for the State of Roraima. Previously, this species was known to occur on the lower Rio Negro and along the Amazon, including the Rio Madeira and the mouth of the Rio Tapajós (Zimmer and Isler 2003). Our records extend the known distribution of *M. klagesi* well into the Rio Branco Basin and more than 300 km northward from previous known sites on the Rio Negro.

**Myrmotherula assimilis* (Leaden Antwren).—AW observed this species in tall *várzea* forest ~20 km north of the mouth of the Rio Branco on 10 June 1990 and several other times in the same general area. In July and October 2001, LNN and MFT, and LNN and JMB, respectively, tape-recorded this species throughout the lower Rio Branco, as far north as the island of Inajatuba, and also along the Anauá and Jauaperí rivers. This species is known to be widespread in flooded forests throughout much of Amazonia (Zimmer and Isler 2003), but was previously unrecorded from the Rio Branco Basin.

**Cercomacra nigrescens* (Blackish Antbird).—MCH tape-recorded this species in Roraima at the mouth of the Rio Branco on 6 July 1999. Subsequently, in July and October 2001, LNN and MFT, and LNN and JMB, respectively, saw and tape-recorded several individuals in mid-successional vegetation on riverine islands and forest edges along both banks of the lower Rio Branco from the

mouth of the river north to the island of Inajatuba where it was fairly common. Additionally, LNN and MFT tape-recorded several individuals along the Paran  da Floresta on the Rio Negro. On 15 October 2006 LNN tape-recorded and collected a pair on the left bank of the Rio Branco (01  31' 06" N, 61  14' 25" W). Three other individuals had been collected earlier by M. P. D. Santos from Viru  National Park and S o Jo o da Baliza in August 2002 and January 2003, respectively. Most of the known range of *C. nigrescens* is restricted to areas south of the Amazon from eastern Colombia to the Brazilian State of Par  (Zimmer and Isler 2003). The only known populations north of the Amazon are represented by the nominate race, which occurs in Surinam, French Guiana, and along the north bank of the Amazon in the Brazilian State of Par  (Pinto 1978, Haverschmidt and Mees 1994). These are the first published records of *C. nigrescens* from the Rio Branco and are separated by ~360 km and more than 600 km from nearest localities to the south and north, respectively, apparently representing a disjunct population.

Cercomacra carbonaria (Rio Branco Antbird).—This taxon was considered to be strictly associated with gallery forests along the upper Rio Branco and some of its tributaries (Stotz 1997, Zimmer et al. 1997, Santos 2003, Zimmer and Isler 2003). In July and October 2001, LNN and MFT, and LNN and JMB, respectively, found and tape-recorded several individuals along the lower Rio Branco where it was locally common in young riverine islands dominated by *Cecropia* spp. In October 2006, LNN and MCH also found the species to be common on riverine islands from Caracara  south to the mouth of the Rio Anau . Our records extend the known range of this species south of Caracara  (previously considered its southernmost limit) to only 13 km north from the mouth of the Rio Branco (01  16' 19" S, 61  50' 21" W). We do not expect to find this species anywhere outside the Rio Branco Basin or in adjacent black-water rivers where successional river islands do not occur. We failed to find *C. carbonaria* in tall *v rzea* forests where *C. nigrescens* was present suggesting that species interactions and habitat preferences may limit its distribution within the Rio Branco Basin. Our records along the

lower Rio Branco suggest that *C. carbonaria* has greater ecological plasticity than previously thought and represent a range extension of more than 300 km southward, doubling the size of its global distribution. At present, *C. carbonaria* is considered Vulnerable to extinction by BirdLife International (2000), but was recently excluded from the Brazilian list of threatened birds (Ministério do Meio Ambiente 2003) based on lack of data. More recently, Vale et al. (in press) suggested downlisting the species to near-threatened, in part due to the significant range extensions here presented.

**Sclateria naevia* (Silvered Antbird).—AW found a vocalizing male 25 km north of the mouth of the Rio Branco on 16 July 1995. Subsequently, LNN and MFT observed and tape-recorded a pair along a dry stream near São João da Baliza at the edge of the Wai-Wai Indian Reservation (01° 05' 21" N, 59° 56' 37" W) in March 2001 and, in October 2006, LNN and MCH found several birds along the Rio Anauá. These are the first records for the region and fill what had appeared as a somewhat inexplicable gap in its distribution (Zimmer and Isler 2003).

Synallaxis propinqua (White-bellied Spinetail).—AW found several individuals vocalizing in early-successional vegetation on a river island 27 km north of the mouth of the Rio Branco on 21 March 1993. One individual was tape-recorded by Pacheco (1995) in October 1993 near the mouth of the Rio Branco. In October 2006, LNN and MCH found several individuals on a young river island along the Rio Branco, opposite the mouth of the Rio Anauá, and on two other river islands. On 14 October 2006 MCH tape-recorded and collected one male on the island of Marari (01° 28' 42" N, 61° 14' 58" W) where two pairs were building nests. Previous to these records, this spinetail was known to occur locally in early-successional growth on river islands along the Amazon River and some of its white-water tributaries (Remsen 2003). Our records not only document the presence of this species in the Rio Branco Basin, but also suggest the presence of a breeding population isolated from the main populations distributed contiguously along the Amazon River and its tributaries.

**Cranioleuca gutturata* (Speckled Spine-

tail).—LNN and JMB found and tape-recorded one individual in mature *várzea* forest at the Niquiá Ecological Station (00° 50' 08" N, 61° 25' 45" W) on 6 October 2001. On 9 October 2006 LNN tape-recorded and collected a male in tall *várzea* forest along the Rio Anauá (00° 57' 20" N, 61° 09' 22" W). These are the first records from the Rio Branco Basin although this species is relatively widespread in Amazonian flooded forests and is present along the lower Rio Negro (Cintra et al. 2007).

**Hemitriccus minor* (Snethlage's Tody-tyrant).—AW saw and tape-recorded one individual 20 km north of the mouth of the Rio Branco on 20 August 1993. Subsequently, MCH found this species in Roraima at the mouth of the Rio Branco in July 1999, and in July and October 2001, LNN and MFT, and LNN and JMB, respectively, found it along most of the lower Rio Branco and other black-water tributaries, including the Água Boa do Univini and Ajaraní rivers (our northernmost locality in Roraima). Our records seem to refer to the race *pallens*, which is a flooded-forest inhabitant common along the middle and lower Rio Negro.

Serpophaga hypoleuca (Riverside Tyrannulet).—AW found a pair on a young river island 27 km north from the mouth of the Rio Branco on 21 March 1993. This species was also recorded on the lower Rio Branco by Pacheco (1995). Prior to these records, this early-successional vegetation inhabitant was known from several white-water rivers in the Amazon Basin, but not from the Rio Branco or the Rio Negro basins (Fitzpatrick 2004).

**Stigmatura napensis* (Lesser Wagtail-tyrant).—AW found a pair in early-successional vegetation on a river island 27 km upstream from the mouth of the Rio Branco on 21 March 1993. On 13 October 2006 MCH and LNN tape-recorded and collected a pair in early successional vegetation on the island of Marari. Several other pairs were located on the same island the following day. The female collected had unshelled eggs in the ovary, suggesting that individuals were reproducing on this island. Prior to our records, the Amazonian form (n nominate race) of this species was known to occur exclusively along white-water Amazonian rivers south of the Amazon, especially on newly-formed sandbars with

bushes of the genus *Tessaria* (Fitzpatrick 2004). We believe this species is absent from the Rio Negro and that birds recorded on the Rio Branco represent an isolated population. Another isolated population was recently found on the upper Orinoco River (Hilty 2003).

**Inezia subflava* (Amazonian Tyrannulet).—AW heard several pairs in flooded vegetation at a lake edge 20 km north of the mouth of the Rio Branco on 23 December 1990 and 23 March 1995. MCH, LNN, and MFT encountered and tape-recorded this species in Viruá National Park in March 2001. Subsequently, in July and October 2001, LNN and MFT, and LNN and JMB, respectively, found *I. subflava* to be fairly common in *várzea* and *igapó* edges along the lower Rio Branco and some black-water tributaries such as the Água Boa do Univini, Iruá, and Jauaperí rivers. Previous specimens from the State of Roraima collected by Natterer (von Pelzeln 1868–1871), Pinto (1966), Emílio Dente (held at Museu Paraense Emílio Goeldi, MPEG), and D. F. Stotz (held at the Field Museum of Natural History) were taken from the upper Rio Branco (and other rivers within the savannas domain) and apparently refer to *I. caudata*, now considered a separate species (Zimmer and Whittaker 2000). Our records represent the first for *I. subflava* on the Rio Branco and in the State of Roraima. *Inezia subflava* (a flooded-forest inhabitant) and *I. caudata* (a gallery forest species) seem to replace each other ecologically and geographically, with the region of turnover somewhere near Caracará.

**Conopias trivirgatus* (Three-striped Flycatcher).—AW saw a pair at the mouth of the Rio Jauaperí on 25 July 1994. Subsequently, AW tape-recorded a few individuals in July 1995 in transitional *várzea* forest ~20 km north of the mouth of the Rio Branco. The distribution of this species is poorly known with several disjunct populations throughout tropical South America (Fitzpatrick 2004).

**Schiffornis major* (Várzea Schiffornis).—AW heard and observed several birds in *várzea* forest near the mouth of the Rio Branco on 7 April 1991. In October 2001, LNN and JMB saw and tape-recorded individuals in tall *várzea* along the lower Rio Branco (00° 50' 08" N, 61° 25' 45" W) and in *igapó* along the

Rio Água Boa do Univini. One bird was collected in Viruá National Park in August 2002 by M. P. D. Santos (held at MPEG) representing the first specimen for the State of Roraima. Several other birds were also heard along the Rio Anauá by LNN and MCH in October 2006 indicating the presence of this species was previously overlooked in the region.

**Hylophilus semicinereus* (Gray-chested Greenlet).—AW heard one bird vocalizing near the mouth of the Rio Branco on 21 December 1990. Subsequently, in July 2001, LNN and MFT observed and tape-recorded several individuals in tall *várzea* and *igapó* forest along the lower Rio Branco and Rio Jauaperí and, in October 2001, LNN and JMB tape-recorded several individuals within the Niquiá Ecological Station and Viruá National Park. On 9 October 2006 LNN tape-recorded and collected a male from a *campinarana-várzea* transition zone on the right bank of the Rio Anauá (00° 57' 33" N, 61° 09' 30" W), finding several other individuals along this river and the Rio Iruá. This species is relatively abundant along the Rio Negro and our records fill a sampling gap in its distribution (Ridgely and Tudor 1989).

Conirostrum bicolor (Bicolor Conebill).—LNN and MFT found and tape-recorded two individuals on a river island (01° 16' S, 61° 50' W) dominated by *Cecropia*. On 6 October 2006 MCH tape-recorded and collected a male from a group of three birds on an early successional river island on the Rio Branco opposite the mouth of the Rio Anauá. LNN and MCH found this species to be abundant on other river islands between Caracará and the mouth of the Rio Anauá suggesting that *C. bicolor* has permanent populations along this stretch of the river. This species has two distinct populations in the Neotropics; one inhabiting mangroves in coastal areas in northern South America and the other inhabiting early-successional vegetation in Amazonia, mainly along the Amazon and some tributaries (Ridgely and Tudor 1989). This species has been previously recorded along the lower Rio Branco by Pacheco (1995) and our records further extend its distribution 260 km to the north, representing the northernmost localities within the Amazon Basin.

**Ammodramus aurifrons* (Yellow-browed

Sparrow).—AW saw two pairs along the edge of a river island 27 km north from the mouth of the Rio Branco on 14 April 1991. Subsequently, in July 2001, LNN and MFT saw and tape-recorded several individuals around the villages of Floresta and Samaúma. In October 2001, LNN and JMB found this species to be locally common along sand-banks and sand-bar scrub on river islands along the lower Rio Branco from the mouth of the river extending to 50 km south of Caracarái (01° 36' 19" N, 61° 13' 27" W). On 13 October 2006, LNN tape-recorded and collected a male on a sandy beach on a river island on the Rio Branco (01° 14' 00" N, 61° 19' 01" W). These records indicate this species is widespread in the region and was previously overlooked due to a sampling gap.

**Sicalis columbiana* (Orange-fronted Yellow-finch).—AW found several individuals along the edge of a river island on the lower Rio Branco on 21 December 1990. Subsequently, in July 2001, LNN and MFT saw and tape-recorded more than 20 individuals at the village of Floresta on the Paraná da Floresta. These seem to represent the first and only records of its occurrence within the Rio Branco Basin and the State of Roraima.

DISCUSSION

Our studies along the lower Rio Branco revealed that south of Caracarái, the avifauna associated with the river floodplains is represented by typical flooded-forest species, similar to those in the Anavilhanas Archipelago and the lower Rio Negro (Cintra et al. 2007). Environmental variables such as soil, flooding regimes, and rainfall differ between the lower Rio Branco and the upper portions of the river where tall *várzea* forests are replaced by gallery forests. Bird species composition on the lower Rio Branco is generally similar to that of other Amazonian rivers, such as the Amazon, Madeira, and the lower Rio Negro. The avifauna of the upper Rio Branco, however, seems to be more closely related to gallery and dry semi-deciduous forests typical of the savannas of northern Roraima, Guyana, and Venezuela. The transition zone between the two habitats seems to be quite abrupt, occurring within the 70-km stretch between Caracarái and the mouth of the Rio Mucajaí, coinciding with the region where savannas re-

place humid forests less than 100 km south of Boa Vista.

Most typical *várzea* bird species such as *Leucopternis schistaceus*, *Monasa nigrifrons*, *Xiphorhynchus kienerii*, *Thamnophilus nigrocinereus*, *Myrmotherula klagesi*, *M. assimilis*, *Myrmoborus lugubris*, and *Hemitriccus minor* seem to reach their northernmost limit in this area. The shift in habitat seems also to be responsible for ecological substitutions between closely related taxa from *várzea* and gallery forests (i.e., *Inezia subflava* and *I. caudata*, and *Ammodramus aurifrons* and *A. humeralis*).

The Rio Branco is unique in representing a white-water river surrounded by black-water drainages including the Negro, Jauaperí, Agua Boa do Univini, Ajarani, and Iruá rivers (Fig. 1). Despite the high similarity between avian communities of the *várzeas* of the Rio Branco and the tall *igapó* of the lower Rio Negro, several elements typical of Amazonian white-water rivers are present on the Rio Branco, but seem to be absent from the entire Rio Negro and its black-water tributaries. We discovered populations of *Cercomacra nigrescens* and *Stigmatura napensis* along the lower Rio Branco, and also confirmed the presence of species previously reported from the mouth of the Rio Branco by Pacheco (1995), such as *Synallaxis propinqua*, *Serpophaga hypoleuca*, and *Conirostrum bicolor*. These species, with the exception of *Cercomacra nigrescens*, which also occurs in *terra firme* forest in part of its range, are typical white-water river-island specialists (Ridgely and Tudor 1989, 1994; Rosenberg 1990; Robinson and Terborgh 1997; Remsen 2003). Repeated records from the area since 1993 suggest these species maintain stable populations locally, rather than representing vagrants or dispersing individuals. Supporting this hypothesis are data that we obtained of unequivocal breeding evidence for *Stigmatura napensis* and *Synallaxis propinqua*.

Most *várzea* birds are believed to be excellent dispersers (Remsen and Parker 1983) and these abilities should be enhanced by having linear and uninterrupted habitats. The existence of isolated populations of white-water specialists along the lower Rio Branco could either be the result of remarkably long-distance dispersal or represent relict populations

from once-continuous habitats. Whether these populations are old or relatively recent, their isolation provides an opportunity for genetic differentiation and endemism in *várzea* forest.

Geomorphological data are still equivocal on past connections of Amazonian rivers, but fish communities of the Rio Branco seem to be more closely related to those of the Amazon River than to those of the Rio Negro (Janzen Zuanon, pers. comm.). Recent Parsimony Analysis of Endemicity (PAE) for characiform fishes produced an area of purported endemism including the Rio Branco, the lower Rio Negro, and the lower Amazon excluding the upper Rio Negro and other portions of the Amazon River (Hubert and Renno 2006). This implies the lower Rio Negro may not be as strong a barrier for these fishes as we believe it is for white-water specialist birds. Rossetti et al. (2005) suggested the existence of a body of water connecting the upper Amazon River and the Rio Branco during the late Pleistocene, a scenario that could explain the existence of recently isolated populations of white-water specialists on the Rio Branco. The extent, age, size, and genetic distinctiveness of these avian populations have not been studied, but represent important data for our overall understanding of the evolutionary history of Amazonian rivers and related flooded forests.

ACKNOWLEDGMENTS

We are particularly grateful to the *Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis* (IBAMA) in Roraima for allowing collecting and access to parks and other conservation units under its jurisdiction. We extend our gratitude to Antonio Galdino and Antonio and Beatriz Lisboa for their support in Caracará, and for inviting us to participate in three expeditions sponsored by the Institute. We also extend our gratitude to A. F. Coutinho Mello, Otacilio de Souza Neves Jr., Inara Rocha Santos, Giovanna Pallazi, and Marina Kluppel for permitting and encouraging our research activities. We are indebted to Reinaldo Barbosa, Vincenzo Lauriola, and Sebastião do Nascimento from INPA in Roraima for providing logistical support in Boa Vista. We thank Luiz Mestre, Catherine Bechtoldt, and Marcelo dos Santos Jr. for their company during some of the field trips. AW thanks Mark Baker of Eco Tours for allowing him the opportunity to travel up the Rio Branco and to conduct field work, and MCH is grateful to Scott Mori and Carol Gracie of the New York Botanical Garden for taking him to the mouth of the Rio Branco for the first time. Sergio Borges, C. E. Braun, Santiago Claramunt,

Jürgen Haffer, Daniel Lane, J. V. Remsen Jr., and an anonymous reviewer made helpful comments on previous versions of the manuscript that greatly improved this paper. LNN had a Conselho Brasileiro de Desenvolvimento Científico e Tecnológico (CNPq)/INPA (DTI) fellowship during the period he developed field work in Roraima in 2003, and a CNPq Overseas Doctoral Fellowship in 2006 (grant #202131/2006-8). Birders Exchange kindly donated optical and recording equipment to the INPA ornithological collection. This article represents Publication 4 in the Amazonian Ornithology Technical Series of the INPA Scientific Collections Program.

LITERATURE CITED

- ALEIXO, A. 2006. Historical diversification of floodplain forest specialist species in the Amazon: a case study with two species of the avian genus *Xiphorhynchus* (Aves: Dendrocolaptidae). *Biological Journal of the Linnean Society* 89:383–395.
- ANDERSON, A. 1981. White-sand vegetation of Brazilian Amazonia. *Biotropica* 13:199–210.
- BARBOSA, R. I. 1997. Distribuição das Chuvas em Roraima. Pages 325–335 in *Homem, ambiente e ecologia no estado de Roraima* (R. I. Barbosa, E. J. G. Ferreira, and E. G. Castellón, Editors). Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil.
- BIERREGAARD, R. O. 1994. Family Accipitridae (hawks and eagles); Slate-colored Hawk species account. Page 168 in *Handbook of the birds of the world. Volume 2. New world vultures to guineafowl* (J. del Hoyo, A. Elliot, and J. Sargatal, Editors). Lynx Edicions, Barcelona, Spain.
- BIRDLIFE INTERNATIONAL. 2000. *Threatened birds of the world*. Lynx Edicions and BirdLife International, Barcelona, Spain.
- BORGES, S. H. AND A. CARVALHAES. 2000. Bird species of black water inundated forests in the Jaú National Park (Amazonas State, Brazil): their contribution to regional species richness. *Biodiversity and Conservation* 9:201–214.
- BROWN, K. S. AND G. T. PRANCE. 1987. Soils and vegetation. Pages 19–45 in *Biogeography and Quaternary history in tropical America* (T. C. Whitmore and G. T. Prance, Editors). Clarendon Press, Oxford, United Kingdom.
- CINTRA, R., T. M. SANAIOTTI, AND M. COHN-HAFT. 2007. Spatial distribution and habitat of the Anavilhanas Archipelago bird community in the Brazilian Amazon. *Biodiversity and Conservation* 16: 313–336.
- COHN-HAFT, M., L. N. NAKA, AND A. M. FERNANDES. In press. Padrões de distribuição da avifauna da várzea do rio Solimões-Amazonas in *Bases científicas para a conservação da várzea: identificação e caracterização de regiões biogeográficas* (A. Albernaz, Editor). Ibama, Brasília, Brazil.
- COMITÊ BRASILEIRO DE REGISTROS ORNITOLÓGICOS. 2006. Lista das aves do Brasil. Online at <http://www.cbro.org.br>. (accessed 1 August 2006).

- FITZPATRICK, J. W. 2004. Family Tyrannidae (tyrant-flycatchers). Pages 170–462 in *Handbook of the birds of the world. Volume 9. Cotingas to pipits and wagtails* (J. del Hoyo, A. Elliot, and D. A. Christie, Editors). Lynx Edicions, Barcelona, Spain.
- GOULDING, M., R. BARTHEM, AND E. J. G. FERREIRA. 2003. The Smithsonian atlas of the Amazon. Smithsonian Institution Press, Washington, D.C., USA.
- HAFFER, J. 1969. Speciation in Amazonian forest birds. *Science* 165:131–137.
- HAFFER, J. 1997. Contact zones between birds of southern Amazonia. *Ornithological Monographs* 48:281–306.
- HAFFER, J. AND J. W. FITZPATRICK. 1985. Geographic variation in some Amazonian forest birds. *Ornithological Monographs* 36:147–168.
- HAVERSCHMIDT, F. AND G. F. MEES. 1994. Birds of Surinam. VACO, Paramaribo, Surinam.
- HILTY, S. 2003. Birds of Venezuela. Second Edition. Princeton University Press, Princeton, New Jersey, USA.
- HUBERT, N. AND J. F. RENNO. 2006. Historical biogeography of South American freshwater fishes. *Journal of Biogeography* 33:1414–1436.
- ISLER, M. L., P. R. ISLER, AND B. M. WHITNEY. 1999. Species limits in antbirds (Passeriformes: Thamnophilidae): the *Myrmotherula surinamensis* complex. *Auk* 116:83–96.
- JUNK, W. R. 1989. Flood tolerance and tree distribution in central Amazon floodplain. Pages 23–46 in *Tropical forests: dynamics, speciation and diversity* (L. B. Holm-Nielsen, I. C. Nielsen, and H. Balsev, Editors). Academic Press, London, United Kingdom.
- KLINGE, H. AND K. FURCH. 1991. Towards the classification of Amazonian floodplains and their forests by means of biogeochemical criteria of river water and forest biomass. *Interciência* 16:196–201.
- MARKS, J. S., R. J. CANNINGS, AND H. MIKKOLA. 1999. Family Strigidae (typical owls). Pages 76–242 in *Handbook of the birds of the world. Volume 5. Barn Owls to hummingbirds* (J. del Hoyo, A. Elliot, and J. Sargatal, Editors). Lynx Edicions, Barcelona, Spain.
- MINISTÉRIO DO MEIO AMBIENTE. 2001. Avaliação e ações prioritárias para a conservação, uso sustentável e repartição de benefícios da biodiversidade na Amazônia Brasileira. (CD-Rom). Instituto Socioambiental (ISA), Brasília, Brazil.
- MINISTÉRIO DO MEIO AMBIENTE. 2003. Lista nacional das espécies da fauna brasileira ameaçadas de extinção. Online at <http://www.mma.gov.br/port/sbf/fauna/grupos3.html> (accessed 15 April 2005).
- NAKA, L. N., M. COHN-HAFT, F. MALLET-RODRIGUES, M. P. D. SANTOS, AND M. F. TORRES. 2006. The avifauna of the Brazilian State of Roraima: bird distribution and biogeography in the Rio Branco Basin. *Revista Brasileira de Ornitologia* 14:197–238.
- NORES, M. 1999. An alternative hypothesis of the origin of Amazonian bird diversity. *Journal of Biogeography* 26:275–285.
- PACHECO, J. F. 1995. New distributional records for some birds from várzea forest at Mamirauá Reserve, western Brazilian Amazonia. *Ararajuba* 3: 83–87.
- PETERMANN, P. 1997. The Birds. Pages 299–314 in *The central Amazon floodplain, ecology of a pulsing system* (W. J. Junk, Editor). Springer-Verlag, Berlin/Heidelberg, Germany.
- PINTO, O. M. O. 1966. Estudo crítico e catálogo remissivo das aves do Território Federal de Roraima. Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil.
- PINTO, O. M. O. 1978. Novo catálogo das aves do Brasil e lista dos exemplares que as representam no Museu Paulista. *Revista Brasileira do Museu Paulista* 22.
- PRANCE, G. T. 1979. Notes on the vegetation of Amazonia. III. The terminology of forest types subject to inundation. *Brittonia* 31:26–38.
- RASMUSSEN, P. C. AND N. J. COLLAR. 2002. Family Bucconidae (puffbirds). Pages 102–138 in *Handbook of the birds of the world. Volume 7. Jacamars to woodpeckers* (J. del Hoyo, A. Elliot, and J. Sargatal, Editors). Lynx Edicions, Barcelona, Spain.
- REMSEN JR., J. V. 2003. Family Furnariidae (ovenbirds). Pages 162–357 in *Handbook of the birds of the world. Volume 8. Broadbills to tapaculos* (J. del Hoyo, A. Elliot, and D. A. Christie, Editors). Lynx Edicions, Barcelona, Spain.
- REMSEN JR., J. V. AND T. A. PARKER III. 1983. Contribution of river-created habitats to bird species richness in Amazonia. *Biotropica* 15:221–231.
- RIDGELY, R. S. AND G. TUDOR. 1989. The birds of South America. Volume 1. The oscine passerines. University of Texas Press, Austin, USA.
- RIDGELY, R. S. AND G. TUDOR. 1994. The birds of South America. Volume 2. The suboscine passerines. University of Texas Press, Austin, USA.
- ROBINSON, S. K. AND J. TERBORGH. 1997. Bird community dynamics along primary successional gradients of an Amazonian whitewater river. *Ornithological Monographs* 48:641–672.
- ROSENBERG, G. H. 1990. Habitat specialization and foraging behavior by birds of Amazonian river islands in northeastern Peru. *Condor* 92:427–443.
- ROSSETTI, D. F., P. MANN DE TOLEDO, AND A. M. GÓES. 2005. New geological framework for western Amazonia (Brazil) and implications for biogeography and evolution. *Quaternary Research* 63:78–89.
- SANTOS, M. P. D. 2003. Novos registros do chororódo-Rio-Branco (*Cercomacra carbonaria*) no estado de Roraima, Brasil. *Atualidades Ornitológicas* 114:3.
- SANTOS, M. P. D. 2004. New records of birds from the Brazilian State of Roraima. *Bulletin of the British Ornithologists' Club* 124:223–226.
- SICK, H. 1967. Rios e enchentes na Amazônia como

- obstaculo para a avifauna. Atas Simposio Biota Amazonia Zoolologica 5:495–520.
- STOTZ, D. F. 1997. Levantamento preliminar da avifauna em Roraima. Pages 581–608 in *Homem, Ambiente e Ecologia no Estado de Roraima* (R. I. Barbosa, E. J. G. Ferreira, and E. G. Castellón, Editors). Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil.
- VALE, M. M., J. B. BELL, M. A. S. ALVES, AND S. L. PIMM. In press. Abundance, distribution, and conservation of *Cercomacra carbonaria* and *Synalaxis kollari*. Bird Conservation International 17: In press.
- VON PELZELN, A. 1868–1871. Zur Ornithologie Brasiliens. Resultate von Johann Natterers Reisen in den Jahren 1817 bis 1835. A. Pichler's Witwe und Sohn, Wien, Austria.
- ZIMMER, K. J. AND M. L. ISLER. 2003. Family Thamnophilidae (typical antbirds). Pages 448–681 in *Handbook of the birds of the world. Volume 8. Broadbills to tapaculos* (J. del Hoyo, A. Elliott, and J. Sargatal, Editors). Lynx Editions, Barcelona, Spain.
- ZIMMER, K. J. AND A. WHITTAKER. 2000. Species limits in Pale-tipped Tyrannulets (Inezia: Tyrannidae). Wilson Bulletin 112:51–66.
- ZIMMER, K. J., A. WHITTAKER, AND D. F. STOTZ. 1997. Vocalizations, behavior and distribution of the Rio Branco Antbird. Wilson Bulletin 109:663–678.