Journal of Ornithology
https://doi.org/10.1007/s10336-020-01850-0

ORIGINAL ARTICLE

Birds of the Juruá River: extensive *várzea* forest as a barrier to *terra firme* birds

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Received: 21 May 2020 / Revised: 25 September 2020 / Accepted: 27 November 2020

Abstract

The Juruá River is the third largest white-water tributary of the Amazon River, yet, historically, it has not been considered an important barrier for bird communities. The upper region of the Juruá River was the focus of two ornithological collections in the early twentieth century, but the middle region, where the river and surrounding *várzea* flooded forest widen, has remained largely unexplored by ornithologists. Inspired by Dr. Emilie Snethlage, whose ornithological expeditions to Amazonian rivers during the early twentieth century were foundational in documenting the importance of river barriers, we undertook a month-long expedition to the middle Juruá River. We collected the first modern specimens, high-quality tissues, and sound recordings of birds from the middle Juruá region. Combining our data with those from previous collections, we present the first comprehensive inventory of bird species from the Juruá region, document several significant range extensions, and report the first evidence that the middle Juruá River acts as a barrier in at least four species complexes of *terra firme* upland forest birds. Our findings have important taxonomic and biogeographic implications for birds of the Juruá region and southwestern Amazon basin.

Keywords Inventory · Amazon forest · Museum collections · Range extensions · Annotated checklist

Zusammenfassung

Vögel des Rio Juruá: ausgedehnte Várzea als Barriere für Vögel der Terra Firme

Der Rio Juruá ist der drittgrößte Weißwasser-Nebenfluss des Amazonas, historisch gesehen jedoch nicht als relevante biogeographische Barriere für Vogelgemeinschaften angesehen. Der obere Teil des Rio Juruá war Ziel zweier ornithologischer Sammlungen zu Beginn des 20. Jahrhunderts, sein mittlerer Teil, wo der Fluss und seine Auen ausgedehnter sind, blieb aber bis 2019 von Vogelexperten weitgehend unerforscht. Inspiriert von Dr. Emilie Snethlage, deren Expeditionen auf Amazonasflüssen im frühen 20. Jahrhundert die Bedeutung von Flüssen als Barrieren zeigten, machten wir eine einmonatige Expedition entlang des mittleren Rio Juruá. Wir sammelten dort die ersten Exemplare, hochwertige Gewebe sowie Tonaufnahmen. Zusammen mit den Daten aus früheren Sammlungen präsentieren wird das bisher umfangreichste Inventar der Vögel des Rio Juruá, dokumentieren Erweiterungen von Verbreitungsgebieten und zeigen, dass der mittlere Rio Juruá eine Barriere für mindestens vier Artkomplexe des Terra-Firme-Waldes ist. Unsere Ergebnisse sind bedeutsam für Fragen der Taxonomie und Biogeographie von Vögeln der Region des Rio Juruá und dem südöstlichen Amazonas.

Communicated by J. T. Lifjeld.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10336-020-01850-0.

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Published online: 02 January 2021

Introduction

Turnover of phylogenetically and ecologically related taxa across the Amazon River and its tributaries is one of the most striking and prevalent biogeographic patterns found in lowland Amazonian birds and other terrestrial vertebrates (Wallace 1852; Bates 1863; Hellmayr 1910; Snethlage 1913; Sick 1967; Naka and Brumfield 2018). Because many bird species from the dark forest understory are reluctant to fly across the rivers (Laurance et al. 2004; Lees and Peres 2009), the limits of species distributions accumulate along them. For example, 54 suboscine taxa (species and subspecies) turnover across the lower Negro River, 45 across the lower Madeira River, and 27 across the lower Tapajós River (M. Rego, unpublished data).

The Juruá River is the third largest white-water tributary of the Amazon River, but it delimits the distributions of relatively few terrestrial taxa (Haffer 1997; Colwell 2000). Peres et al. (1996) found genetic and morphological evidence that the Juruá River separates *Sanguinus fuscicollis fuscicollis* from *S. f. melanoleucus*, but most studies have found that taxon turnover occurs between the upper and lower reaches of the river instead of across it. For example, Haffer (1997) noted several species pairs (e.g., *Galbalcyrhynchus purusianus*/*G. leucotis*, and *Pipra filicauda*/*P. fasciicauda*) that replace each other between the northern and southern parts of the Juruá, but did not find any species pairs delimited by the river itself. An extensive inventory of non-volant mammals found that clades are sharply divided into upriver and downriver groups along the Juruá, rather than right bank and left bank forms (Matocq et al. 2000; Patton et al. 2000). Gascon et al. (2000) found that geographic distance and habitat type, rather than riverbank association, were better predictors of community similarity. For some *terra firme* forest birds, the Juruá river does not seem to mitigate gene flow (Ribas et al. 2018; Silva et al. 2019; Azuaje-Rodríguez et al. 2020). However, the lack of ornithological surveys and museum specimens along the lower and middle reaches of the Juruá prevents a comprehensive assessment of the role of the Juruá as a biogeographical barrier.

Our knowledge of bird distributions along the Juruá stems primarily from collections made in the first half of the twentieth century. The first bird collection in the region was conducted by Ernest Garbe and his son Walter Garbe in 1901 and 1902. They collected 399 individuals of 184 different species, now archived at the Museum of Zoology of the University of São Paulo (Ihering 1904). A second more complete collection was made by the Olallas and their assistants during 1936 and 1937. The Olallas collected 4518 specimens comprising nearly 400 species, now housed at the Museum of Zoology of University of São Paulo and at the Swedish Royal Museum of Natural History in Stockholm (Gyldenstolpe 1945). Both the Garbe's and the Olalla's collections focused primarily along the upper reaches of the Juruá River, in areas within the current municipality of Eirunepé (Fig. 1).

In the second half of the twentieth century, other noteworthy ornithological surveys occurred in the upper reaches of the Juruá. In 1956, Fernando Novaes, working for the Goeldi Museum, collected 363 specimens of 179 bird species along the Juruá in the Brazilian state of Acre (Novaes 1957, 1958). In the 1990s, three expeditions that focused on all terrestrial vertebrate groups surveyed primarily along the upper Juruá (Whittaker and Oren 1999). Whittaker, Oren, and collaborators built an extensive collection of 895 bird specimens (Whittaker and Oren 1999; M. Rego unpublished data). In the 2000s, an inventory was made, again in the headwaters, in *campinas* and *campinaranas* sand-forest habitats confined to the upper Juruá (Guilherme and Borges 2011). Most recently, Guilherme (2016), in a comprehensive inventory of birds of the state of Acre, listed the birds collected and observed around the Municipality of Mâncio Lima, again in the upper Juruá (Whittaker et al. 2002). The few ornithological expeditions to the Juruá River over the past century have all surveyed the headwaters and upper region of the river, where, because of its diminished width and less extensive flooded forests, it is a less effective barrier for terrestrial organisms (Novaes 1957, 1958; Peres et al. 1996; Whittaker and Oren 1999; Guilherme 2016).

Here, we present the results of a one-month expedition to the middle Juruá made in honor of Dr. Emilie Snethlage (1868–1929), a pioneering ornithologist whose work was seminal in understanding the influence of Amazonian rivers on bird distributions (Snethlage 1913). Despite Snethlage's extensive work in the Amazon Basin, she was never able to explore the Juruá River. Combining data from this trip with species lists from the Garbes, Olallas, Novaes, Whittaker, Oren, and Guilerme collections (Ihering 1904; Gyldenstolpe 1945; Novaes 1957; Whittaker and Oren 1999; Guilherme 2016), we present a comprehensive list of the avifauna of the Juruá river basin. One of the most notable results is that the middle Juruá and its wide *várzea* (flooded forest) act as a biogeographic barrier for at least four species complexes of *terra firme* (upland forest) birds.

Methods

Study area

The Juruá flows along a linear distance of 1000 km, from over 453 m above sea level at its headwaters to 43 m at its mouth. The river's origin is in the Ucayali department in Peru, and most of its course crosses Brazilian territory,

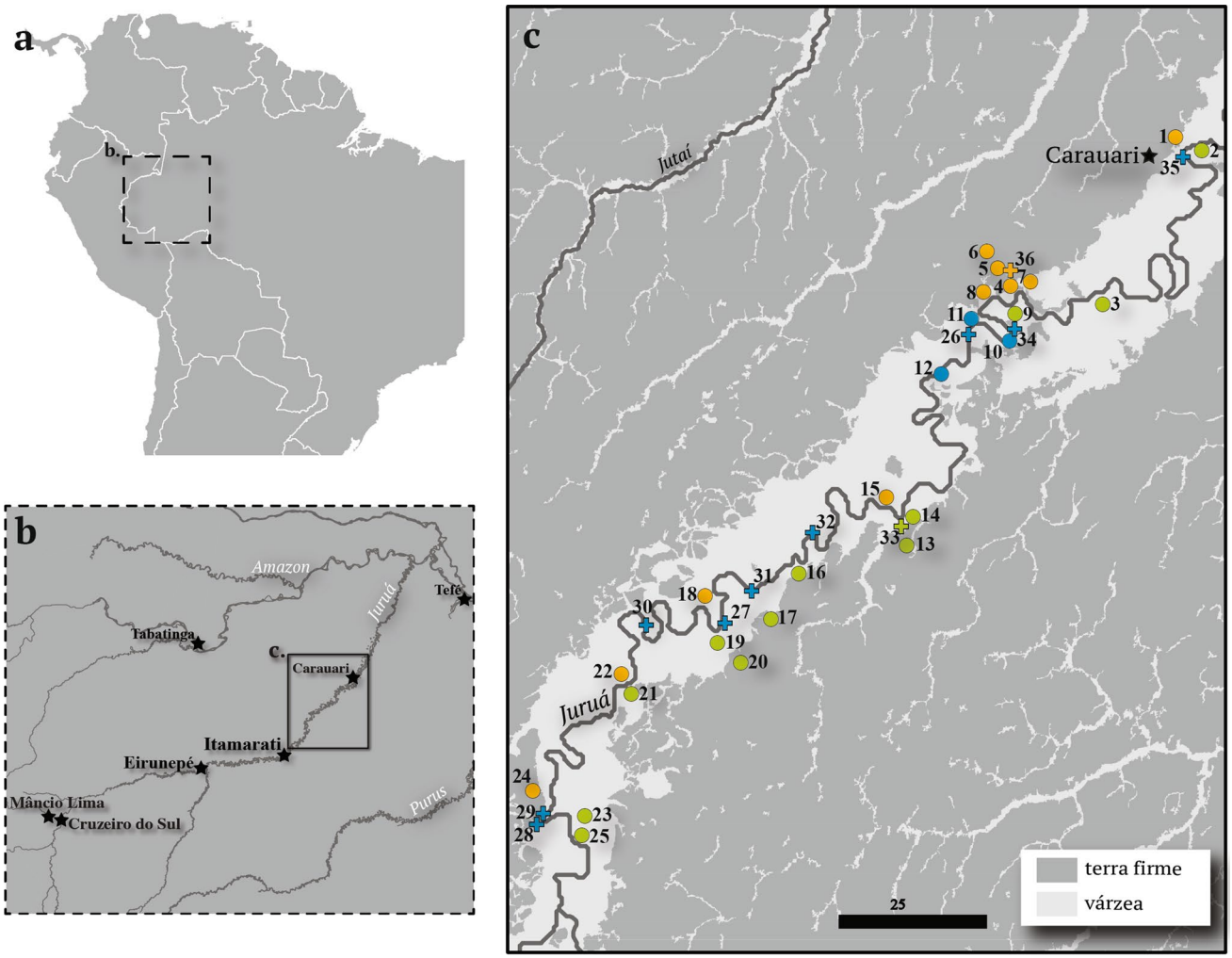

Fig. 1 **a** Study area in western Amazonia. **b** Detail of area in dashed square depicted in A. **c** Detail of black rectangle depicted in B: localities sampled along the Juruá River. Green symbols represent localities on the right bank, orange symbols represent localities on the left bank, and blue symbols represent localities along the river. Circles represent localities where we collected specimens. Crosses represent localities that were observation only (*várzea/terra firme* layer obtained from Hess et al. 2015)

in the states of Acre and Amazonas (Oppenheim 1937). The Juruá is one of the most sinuous rivers in the Amazon Basin with a total course length of approximately 3283 km (Oppenheim 1937). The river's course is markedly dynamic with channels and oxbow lakes surrounding the main course (Gascon et al. 2000; Lima et al. 2014). At its headwaters, the Juruá is no wider than tens of meters, but at its mouth, it is approximately 500 m in width. The flooded *várzea* forests along the river are ~ 5 km wide at the headwaters and approximately 29 km wide near the mouth (measures inferred from geographical layers made available by Hess et al. 2015). Differently from other Amazonian Rivers, the Juruá does not seem to have river islands (Chandless 1869).

Fieldwork

From August 10 to September 4, 2019, we sampled 25 localities along the Juruá River between the municipalities of Carauari and Itamarati (Table S1, Fig. 1). We conducted surveys along transects that followed preexisting trails. We tallied all birds seen or heard, recorded habitat associations, and made audio recordings. We deposited observational data in the Avian Knowledge Network through the eBird portal (Cornell Laboratory of Ornithology, Ithaca, New York, USA). Audio recordings were archived at the Macaulay Library (ML) at the Cornell Laboratory of Ornithology. In 17 of the 25 localities, we set up from 10 to 50 mist nets (12 m long, 3 m tall) that were open from 5 am to 12 pm for

20 field days (140 h/net). We also used shotguns to collect birds, particularly canopy species. Because of the river's meandering course, we use 'left bank' and 'right bank' instead of 'west bank' and 'east bank', respectively (Fig. 1). We made observations and collected birds from 12 localities on the right bank of the Juruá, from ten localities on the left bank, and from three localities along the river's course. We made observations from nine additional localities from river-edge environments and from one locality on the right bank of the Juruá River. In total, we conducted ~ 3700 h of mist-net effort (number of localities × number of nets × period when nets were operating) on the right bank of the Juruá and ~ 2800 h on the left bank. The time difference in mist-net effort between riverbanks is due to fewer accessible *terra firme* areas on the left bank of the river during the dry season.

We prepared all specimens in the field as study skins, and preserved pectoral muscle, heart, and liver tissues in liquid nitrogen and 100% ethanol. For each specimen, we collected data on reproductive condition, molt stage, skull ossification, stomach contents, presence of bursa of Fabricius, soft part colors, presence of fat, and parasites. Voucher specimens and tissues are archived in the Museum of Zoology of University of São Paulo and the Museum of Natural Science of Louisiana State University. We identified birds to the species level using the taxonomy of the International Ornithological Congress (IOC) World Bird List (Gill et al. 2020). When possible, we identified specimens to subspecies based on Dickinson and Remsen (2013) and Dickinson and Christidis (2014).

Occurrence maps

We produced occurrence maps for each species by georeferencing specimen records from the following collections: Louisiana State University Museum of Natural Science (LSUMNS), Museu Paraense Emílio Goeldi (MPEG), Academy of Natural Sciences of Drexel University (ANSP), Carnegie Museum of Natural History (CNMH), William Phelps Ornithological Collection (COP), Field Museum of Natural History (FMNH), Instituto Alexander von Humboldt (IAvH), Instituto Nacional de Pesquisas da Amazônia (INPA), University of Kansas Biodiveristy Institute (KU), Natural History Museum of Los Angeles County (LACM), Museum of Comparative Zoology of Harvard (MCZ), Museum of Vertebrate Zoology of Berkeley (MVZ), Museum of Zoology of University of São Paulo (MZUSP), Royal Ontario Museum (ROM), Universidade Federal do Mato Grosso (UFMT), University of Michigan Museum of Zoology (UMMZ), National Museum of Natural History (NMNH), Yale Peabody Museum (YPM), Instituto de Ciencias Naturales (ICN) de la Universidad Nacional de Colombia, American Museum of Natural History (AMNH), Universidade Federal de Pernambuco (UFPE), Museum of Southwestern Biology (MSB), Moore Laboratory of Zoology (MLZ), Rijksmuseum van Natuurlijke Historie (RMNH), and Zoological Museum of Amsterdam (ZMA). Specimen data are available online through GBIF (2020) and VertNet (http://vertnet.org), or by contacting the museums directly.

Morphological comparisons

We compared series of specimens from the same species complex collected from different localities along the river course and from different river banks. We made visual comparisons of plumage patterns and used the Munsell catalog to assess differences in shades of plumage hue. We examined Juruá specimens housed in the Museum of Zoology of University of São Paulo to check identification and additional details.

Results

We recorded 429 bird species from 68 bird families, and collected 913 specimens of 226 species. We collected 377 specimens of 108 species on the left bank and 522 bird specimens of 190 species on the right bank. Fourteen specimens were collected along the river course and were not associated with a specific riverbank. We collected 323 specimens of 128 species in *várzea* and riverine edge environments and 591 specimens of 138 species in *terra firme* forest (Table S2).

Taxon replacements across the Juruá River

Epinecrophylla h. haematonota and *E. a. amazonica*

E. haematonota is the sister group to the clade formed by *E. amazonica* and *E. spodionota* (Johnson et al. 2020). Although they are not sister taxa, both *E. h. haematonota* and *E. a. amazonica* occur in western Amazonia, but the distribution limits between the two taxa were unknown. The Juruá River was the suggested barrier between the two groups, but such information could not be confirmed due to the lack of precise locality information for the type series of *E. a. amazonica* (Ihering 1904; Johnson et al. 2020).

We collected nine *Epinecrophylla* specimens (seven males and two females) from the left bank of the Juruá River (localities 5, 6, and 24). These specimens differ in plumage characteristics from the 16 specimens (ten males, five females, and one undetermined sex) collected from the right bank (localities 13, 17, and 20) (Fig. 1).

We identified specimens collected on the left bank as *E. h. haematonota* following the original description of Sclater (1857), the type specimens of which were collected in Peru

along the Huallaga River (Zimmer 1932). Our specimens collected from the right bank were identical in plumage to the type series of *E. a. amazonica* housed at the Museum of Zoology of University of São Paulo. Ihering (1904) described *E. a. amazonica* based on specimens from the Juruá River collected by the Garbes, who did not note from which river bank these specimens were collected, but we assume that they came from the right bank.

Both Sclater's and Ihering's original descriptions lacked details regarding diagnostic plumage patterns between *E. h. haematonota* and *E. a. amazonica*. In examining morphological differences between *haematonota* and *amazonica*, Zimmer (1932) noted slight variation in overall plumage coloration between birds from the east bank of the Ucayali River in Peru and birds from the Madeira River and Tefé in the Brazilian Amazon. Zimmer retained the name *E. h. haematonota* for the Peruvian birds, and although he never inspected Ihering's specimens from the Juruá, he grouped the Madeira River and Tefé specimens with *E. a. amazonica.* Zimmer mentioned that females of *E. a. amazonica* showed less white and a deeper shade of ochraceous on the throat than *E. h. haematonota*. Peters (1951) stated that *E. a. amazonica* occurs on both the left and right banks of the Juruá River. However, our data suggest that *E. h. haematonota* and *E. a. amazonica* are separated by the Juruá River, at least along its middle course. Guilherme (2016) reported that *E. h. haematonota* occurs on both banks of the upper Juruá, in the Acre state, indicating that it should be in contact with *E. a. amazonica* somewhere in the upper Juruá-Purús region.

In the Juruá specimens we examined (including Garbe's and Olallas' specimens deposited at MZUSP), *E. h. haematonota* (left bank) males have thin white stripes on the throat area, whereas *E. a. amazonica* (right bank) have conspicuous white triangular markings on the throat and chin (Fig. 2). Females of *E. h. haematonota* have a white chin and throat with dark brown stripes extending to the chest area, where these marks intergrade with buff orange stripes. Female specimens of *E. a. amazonica* have buff orange throat with buff brown stripes that do not extend to the chest area (Fig. 2).

Willisornis poecilinotus gutturalis and *W. p. griseiventris*

We collected seven specimens of *Willisornis poecilinotus* (four males and three females) on the left bank (localities 1, 5, and 6), and 19 specimens (11 males and 8 females) on the right bank (localities 13, 17, and 20). Birds from the left bank are *Willisornis poecilinotus gutturalis* and birds from the right bank are *W. p. griseiventris*. Males of *W. p. gutturalis* and *W. p. griseiventris* are similar in plumage except for throat color, which is black in *W. p. gutturalis* and gray in *W. p. griseiventris* (Fig. 2). The females differ more conspicuously. Female *W. p. gutturalis* have brown underparts with an olive brown chest and belly and an orange brown throat; the posterior upperparts are black with broad white

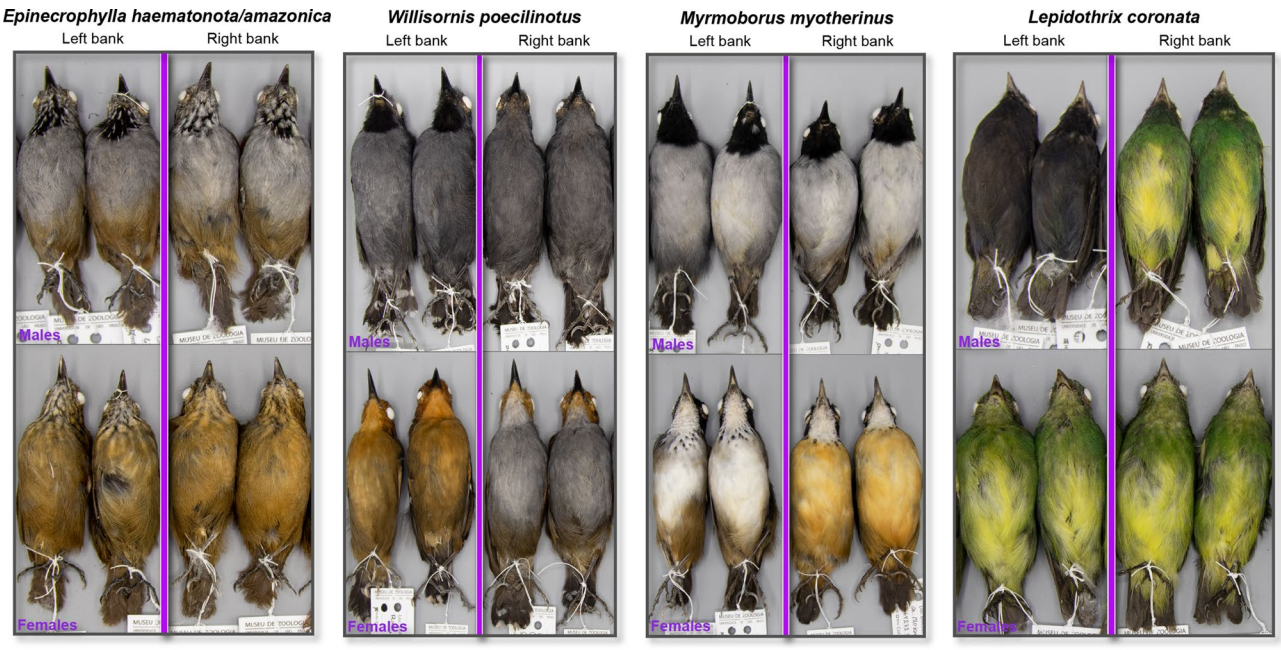

Fig. 2 Four pairs of bird taxa that show differences in plumage patterns across the middle Juruá River. Specimens from opposite river banks are separated by the purple line. Males are shown on the top row and females on the bottom row

edges, forming the characteristic scaled pattern. Female *W. p. griseiventris* have gray underparts with a whitish throat; the upperparts are olive brown lacking the white streaks. According to Isler and Whitney (2011), the eastern limit of *gutturalis*' distribution is unknown, although the Juruá River was speculated to be the most probable barrier (Peters 1951; Haffer 1997). Our collection, combined with the specimens collected at Eirunepé (Ihering 1904) and at Rio Eiru (Gyldenstolpe 1945), corroborates the Juruá as the boundary between *W. p. gutturalis* and *W. p. griseiventris*, at least along the lower and middle reaches of the river. Guilherme (2016) reported *W. p. griseiventris* on both banks of the upper Juruá, in Acre, suggesting that both *Willisornis* taxa might be in contact somewhere along the left bank of the Juruá, in Amazonas state.

Myrmoborus myotherinus ssp. and *M. m. myotherinus*

We collected eight specimens (five males and three females) on the left bank (localities 1, 5, 6, and 24), and four specimens (two males and two females) on the right bank (locality 20). Males were essentially identical in plumage on both banks of the river, but females showed conspicuous color differences between river banks (Fig. 2). Females from the left bank have white underparts, olive brown flanks, and long, slender black marks extending from the bottom of the throat to the chest, whereas females from the right bank have yellow-buff underparts, black spots on the lower throat, and a white throat and chin, typical of *M. m. myotherinus*. The white plumage typical of females from the left bank is only observed in the subspecies *M. m. incanus*; however, *M. m. incanus* is distributed disjunctly on the north bank of the Amazon River, between the Japurá and Içá Rivers. We are unable to identify the left bank *M. myotherinus* as any described subspecies, so we are working on the molecular systematics of *M. myotherinus* to assess its taxonomic status. According to Guilherme (2016), *M. m. myiotherinus* occurs on both banks of the upper Juruá, suggesting that *M. m. myiotherinus* and *M. myiotherinus* ssp. might be in contact somewhere on the left bank along the middle Juruá.

Lepidothrix c. coronata and *L. c. caelestipileata*

We collected 17 specimens (seven males and 10 females) of *Lepidothrix coronata* from the left bank (localities 1, 5, 6, and 24), and five specimens (three males and two females) from the right bank (localities 17 and 20). Females did not differ in plumage characteristics across the river. In contrast, males from the left bank were black with a glossy blue crown, but the three adult males from the right bank had vivid green upperparts, chest, and flanks, black throat and lores, yellow in the central breast and belly, and a blue crown (Fig. 2). We identified the left bank specimens as *L. c. coronata*, which occurs in NE Peru and adjacent W Brazil and S Amazon, and specimens collected on the right bank as *L. c. caelestipileata*, which occurs in NW Bolivia and adjacent W Brazil (Snow 2004). These specimens provide evidence that the middle Juruá River is a barrier to *L. c. coronata* and *L. c. caelestipileata*, which is corroborated by molecular evidence (Reis et al. 2020). Guilherme (2016) reported black males in the upper Juruá, which suggests that *L. c. coronata* and *L. c. caelestipileata* are in contact somewhere within the Juruá–Purus interfluve. The possible contact zone between two clades of *L. coronata* in the Juruá–Purus was also suggested by Reis et al. (2020).

Taxon replacements along the Juruá River

Galbalcyrhynchus purusianus and *G. leucotis*

On 31 August 2019, we collected one male *Galbalcyrhynchus purusianus* in tall, mature *várzea* forest on the right bank. We did not record *G. leucotis*, which is expected to replace *G. purusianus* further downstream, close to the Solimões River (Rego et al. unpublished data).

Galbula cyanescens and *G. tombacea*

From 21–31 August 2019, we collected three males and five females of *Galbula cyanescens* in *várzea* forest. The northern limit of *G. cyanescens* is unknown, but it seems to be replaced by *G. tombacea* at the lower Juruá River. We did not record *G. tombacea* at any of our study sites. Our data suggest that *G. cyanescens* occurs along the middle Juruá (Haffer 1974, 1997).

Capito auratus amazonicus and *C. a. orasae*

From 10 to 19 August 2019, we collected three individuals (two males and one female) of *Capito auratus amazonicus* in *terra firme* forest. We did not record *C. a. orasae*, which was collected from the right bank of the Juruá ("Rio Eiru") by the Olallas (Gyldenstolpe 1945). We suggest that *C. a. orasae* replaces *C. a. amazonicus* at some point between the municipalities of Itamarati and Eirunepé (Rego et al. unpublished data; Guilherme 2016).

Pipra filicauda and *P. fasciicauda*

From 25 to 30 of August 2019, we collected five individuals (three males and two females) of *Pipra filicauda* in the understory of *várzea* forest on both banks of the Juruá. We did not observe or collect *Pipra fasciicauda*, but *P. fasciicauda* should replace *P. filicauda* at the headwaters of the Juruá (Rego et al. unpublished data; Haffer 1997; Guilherme 2016).

New records for the middle Juruá and range extensions for riverine species

Neochen jubata

On 19 August 2019, we collected two *Neochen jubata* from a sand beach with grass stands on the right bank of the Juruá River. Although not collected by the Garbes or Olallas, we found these birds to be abundant along the entire river course (Table S2), as also noted by Whittaker and Oren (1999). *Neochen jubata* is reportedly a migratory species (Davenport et al. 2012) that may leave the Juruá during the rainy season when the beaches disappear. Neither individual we collected had enlarged gonads, and the female had a convoluted oviduct, indicating that the bird had long passed the breeding period. Neither bird was molting flight feathers, but each had a few pin feathers on their chest, head, mantle, and belly.

Anhima cornuta

On 28 August 2019, we collected one *Anhima cornuta* on the edge of *várzea* forest by the side of an oxbow lake (Fig. 3). We observed this species at several other localities, especially in grasslands near sand beaches (Table S2). These are the first reports of this species for the Juruá in the Amazonas state. This species was not on previously mentioned lists (Ihering 1904; Gyldenstolpe 1945; Novaes 1957, 1958; Whittaker and Oren 1999), but *A. cornuta* was seen at RESEX *Alto Juruá* in the upper Juruá river (Whittaker et al. 2002; Guilherme 2016). Our specimen is the first of this species collected along the Juruá River.

Laterallus exilis

On 28 August 2019, we netted one specimen of *Laterallus exilis* in river-edge habitat with scattered *Cecropia* and dense grass stands. This specimen represents the first record for the middle Juruá River (Ihering 1904; Gyldenstolpe 1945). Two other specimens were collected from the upper Juruá (Guilherme 2016).

Vanellus chilensis

We observed *Vanellus chilensis* at several localities along the river and in open areas adjacent to communities. This species was not mentioned in Juruá inventories before 2016 (Ihering 1904; Gyldenstolpe 1945; Novaes 1957; Whittaker and Oren 1999). Guilherme (2016) noted that the species arrived recently to the state of Acre. Locals reported to us that *V. chilensis* colonized the middle Juruá during the last 5 years, probably due to deforestation for ranching.

Certhiaxis cinnamomeus

We collected a female specimen of *Certhiaxis cinnamomeus* on 28 August 2019 from river-edge habitat with scattered *Cecropia* and dense grass stands. This represents a new record for the Juruá River and a new record for the area in between the Madeira and Solimões Rivers (Ihering 1904; Gyldenstolpe 1945; Novaes 1957, 1958; Whittaker and Oren 1999; Guilherme 2016).

Knipolegus poecilocercus

We audio-recorded and collected one specimen of *Knipolegus poecilocercus* on the right bank of the Juruá River on 21 August 2019 in low forest surrounding boggy grasslands adjacent to the Chué water course (Fig. 3). The only previous records for *K. poecilocercus* from western Brazil were from between the Madeira and the Solimões Rivers, where four specimens were collected by the Olallas in the 1930s. Of those, three were collected from the upper left bank of the Juruá and one from the upper right bank (Eirunepé municipality) (Gyldenstolpe 1945).

Turdus amaurochalinus

We collected three specimens of *Turdus amaurochalinus*. The birds were not vocal. At locality 16, the birds were netted in low *várzea* forest adjacent to boggy grassland. In locality 18, the bird was netted in grassland adjacent to *várzea* forest (Fig. 3). These specimens are the first ones from the middle Juruá River. Other specimens reported for the Juruá were collected around the municipality of Cruzeiro do Sul, in Acre (Guilherme 2016).

Sporophila americana

We collected four specimens of *Sporophila americana* from boggy grasslands around an oxbow lake and grassland adjacent to *várzea* forest. These records represent a westward extension of the distribution of this species, making it parapatric with its sister species *S. murallae*, which occurs in the upper Juruá (Guilherme 2016). All specimens were identified as *S. americana* with no evidence of intermediacy or plumage introgression with *S. murallae*.

Sporophila nigricollis

We collected the female of a pair of *Sporophila nigricollis*. The identification of the male was obvious in the field due to its yellowish belly, but the identification of the female

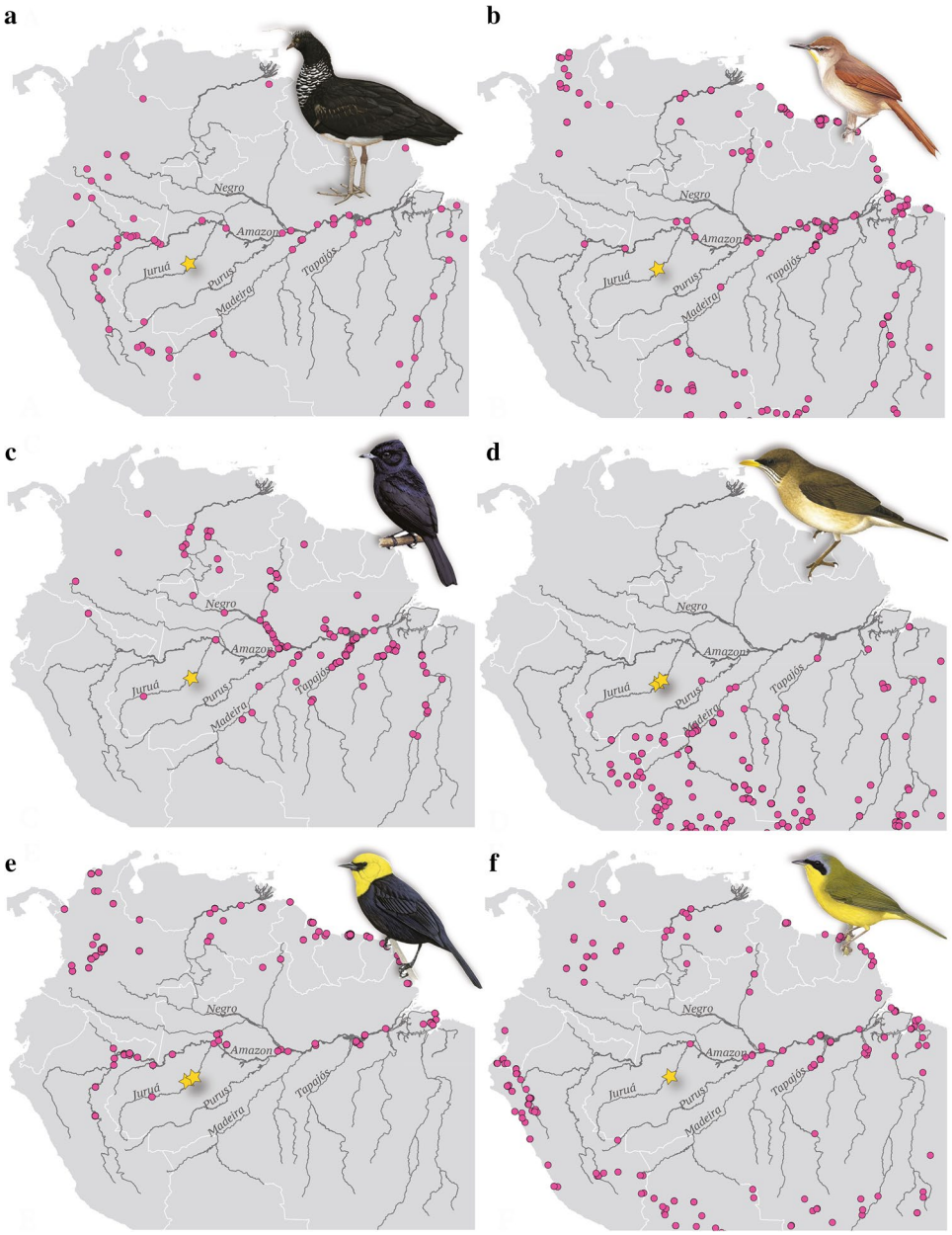

Fig. 3 New records for the middle Juruá. Pink circles represent localities where specimens were collected historically. Yellow stars represent the localities where we collected specimens. **a** *Anhima cornuta,* **b** *Certhiaxis cinnamomeus,* **c** *Knipolegus poecilocercus,* **d** *Turdus amaurochalinus,* **e** *Chrysomus icterocephalus, and* **f** *Geothlypis aequinoctialis. Illustrations reproduced by permission of Lynx Edicions*

rests on the assumption that it was mated to the male. This record fills a large gap in its western Amazonia distribution between the Purus and Amazon Rivers. This represents the first published record of this species for the Juruá River (Ihering 1904; Gyldenstolpe 1945; Novaes 1957; Whittaker and Oren 1999; Whittaker et al. 2002; Guilherme 2016).

Chrysomus icterocephalus

We collected three specimens of *Chrysomus icterocephalus* from the right bank of the Juruá River. Groups of this species were visually recorded several times in grasslands near oxbow lakes (Table S2; Fig. 3). Two females were collected at the edge of *várzea* forest surrounded by boggy grasslands near an oxbow lake. We netted one male at locality 9 in grasslands adjacent to *várzea* forest and river sand beach. Both the Garbes and Olallas collected few specimens of *C. icterocephalus* around Eirunepé. Our specimens represent the only records from between the Amazon River and the Juruá headwaters.

Geothlypis aequinoctialis aequinoctialis

We collected one specimen of *Geothlypis aequinoctialis* in tall grassland between the sandy beach and *várzea* forest

on the Juruá. This species is poorly known in southwestern Amazonia, with only a few records of the subspecies *G. a. velata* from the upper courses of the Purus, Madre de Dios, and Ucayali Rivers (Fig. 3). Our specimen is the first ever collected along the Juruá, and represents the second record of *G. a. aequinoctialis* for the river. Whittaker and Oren (1999) observed one individual on the left bank of the Juruá, 55 km W of the municipality of Itamarati. We identified our specimen as *G. a. aequinoctialis*, because plumage surrounding the black mask was olive green instead of gray as in *G. a. velata*.

Bamboo avifauna

We found small patches of *Guadua* bamboo at two localities: along the river at locality 7 and alongside *terra firme* at locality 20. In this habitat, we documented several species commonly found in bamboo, including *Pheugopedius genibarbis*, *Myrmoborus leucophrys*, and *Automolus rufipileatus* (Lebbin 2013). Although we collected one pair of the bamboo-associated species *Ramphotrigon megacephalum* (Kratter 1997), we found no obligate bamboo species in either *Guadua* bamboo patch. This may have been because the bamboo patches were small and possibly young. Although our observations suggest that the middle Juruá lacks adequate habitat for bamboo specialists, its headwaters harbor several obligate species of bamboo birds (Parker et al. 1997; Guilherme and Santos 2009). To determine the northern extent of these species, and how bamboo communities shift from obligate to facultative species in more northern localities, more intensive surveys of the bamboo habitat near Eirunepé are necessary.

Discussion

The collection and observations we made represent the first modern ornithological inventory for the middle Juruá River. We observed seven species that were not recorded from previous expeditions, and collected 11 species not collected previously along the Juruá River (Ihering 1904; Gyldenstolpe 1945; Novaes 1957, 1958; Whittaker and Oren 1999; Guilherme 2016).

Historically, the Juruá has not been found to act as biogeographical barrier for terrestrial animals (Patton et al. 1994; Gascon et al. 2000; Ruokolainen et al. 2018, 2019). The Juruá is not wide, is highly meandering, and has a history of lateral river channel migration, and shifts within its alluvial plain (Brasil 1977; Stølum 1996). Such natural movements of land masses from one bank to the other would facilitate gene flow between previously allopatric bird species, breaking the typical barrier effect characteristic of many Amazonian Rivers (Peres et al. 1996).

Our comparisons of plumage patterns of conspecifics collected from both river banks suggest that the Juruá is not a barrier for most of the bird taxa we examined. However, we found four taxon pairs (*Epinecrophylla haematonota*/*E. amazonica*, *Willisornis poecilinotus gutturalis*/*W. p. griseiventris*, *Myrmoborus myotherinus* ssp./*M. m. myotherinus*, and *Lepidothrix coronata coronata*/*L. c. caelestipileata*) that show marked plumage differences across riverbanks at the middle course of the Juruá River. These bird species are typical occupants of the *terra firme* understory and have low dispersal ability.

Our field observations, combined with Landsat satellite imagery (Landsat image courtesy of the U.S. Geological Survey) and other GIS layers for the region (Hess et al. 2015), suggest that the most frequent river capture events in the middle Juruá are restricted to the flooded forest (*várzea*) (Fig. 4). This may explain why the river is a barrier to some *terra firme* species. In the areas we visited, the Juruá River was only ~ 400 m wide; however, the distance between *terra firme* forest on opposite river banks was, on average, 20 km. Our data suggest that some birds that are exclusively linked to *terra firme* are still isolated on opposite river banks, despite the constant river captures. Thus, the extensive *várzea* appears to act as a barrier. On the other hand, depending on the magnitude and age of a river capture event, white sand forest, such as *campinas* and *campinaranas* might be formed, which could also contribute to the geographic isolation of *terra firme* birds (Rossetti et al. 2019). However, we failed to detect *campinas* and *campinaranas* along the middle Juruá, and Chandless (1869) mentioned that these formations are absent in the region. A detailed study of genetic structure in several *terra firme* species' complexes distributed across the Juruá River is the subject of ongoing work.

Although not historically considered a river barrier for bird species, the Juruá is known to have north/south species replacements along its course (Haffer 1997). Some north/south replacement examples are *Galbula tombacea*/*G. cyanescens*, *Galbalcyrhynchus purusianus*/*G. leucotis*, and *Pipra filicauda*/*P. fasciicauda* (Haffer 1997). We did not sample birds from within any potential north/south contact zone, but did make some progress in locating where those contact zones occur. Most are expected to coincide with the transition between *dense tropical forest* found in the lower reaches of the river and *open tropical forest* found in its upper reaches (Silva et al. 1992). The transition is presumably due to distinct underlying soil formations (Brasil 1977; Daly and Prance 1989; Haffer 1997; Patton et al. 2000) associated with the Iquitos Arch, a Pre-Cambrian zone of uplift that is not part of contemporary topography, but which delimits phytogeographic units across western

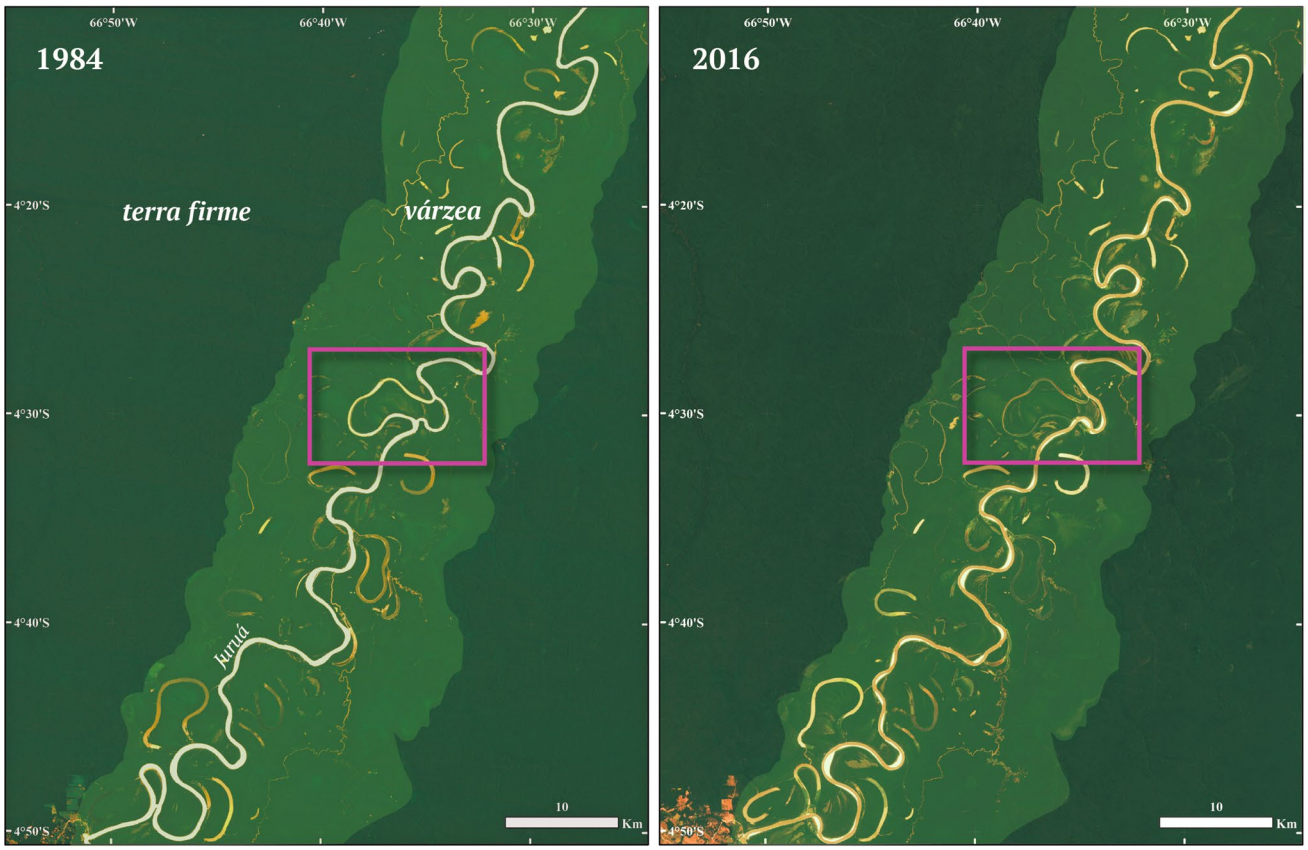

Fig. 4 Satellite imagery of the same part of the Juruá River in 1984 (left panel), and 2016 (right panel), from Landsat 5 and 8, respectively (Landsat image courtesy of the U.S. Geological Survey). Pink box shows a part of the river that moved from the right bank to the left bank in the last 33 years. Notice that the landmass that is captured is exclusively within *várzea* forest (Hess et al. 2015)

Amazonia (Putzer 1984; Roddaz et al. 2005). According to Tuomisto et al. (2019), the areas that we sampled belong to the Içá floristic formation, within the Central Amazon fluvial deposition system, which is north of the Iquitos Arch. The Içá formation is replaced by the Solimões formation between Itamarati and Eirunepé, and by the bamboo forest formation in Acre (Tuomisto et al. 2019). Because contact zones usually concentrate around areas of climatic, soil, and vegetation transitions, sampling birds between Itamarati and Eirunepé could help pinpoint the location of contact zones (Rasanen et al. 1987).

Together, our observations for the middle Juruá and Guilherme's (2016) observations from the narrow headwaters suggest that *Epinecrophylla haematonota/amazonica*, and subspecific forms of *Willisornis poecilinotus*, *Myrmoborus myotherinus,* and *Lepidothrix coronata* come into contact somewhere in Amazonas state. In the upper Juruá, where both the river and the *várzea* floodplain are narrower than downstream, contact seems very likely (Haffer 1997; Naka et al. 2012; Weir et al. 2015; Guilherme 2016; Naka and Brumfield 2018; Reis et al. 2020). Thus, the headwaters of the Juruá could accumulate contact zones between species occurring on both sides of the Iquitos Arch (horizontal contact zones), and also contact zones between taxa occurring on different river banks downstream (vertical contact zones). Further field and molecular work are necessary to assess whether genetic exchange occurs at these putative contact zones.

Many of the new records we documented are of riverine species. The meandering nature of the Juruá River undoubtedly contributes to the abundance of river-created habitats (e.g., blackwater lakes, marshes, and beach habitat), and thus, the abundance of several species restricted to river-created habitats (Remsen and Parker 1983). For example, despite the narrowness of the river and lack of typical white-water river islands, we found many taxa along the Juruá known to be associated with ephemeral river islands (Remsen and Parker 1983; Rosenberg 1990), including *Myrmotherula assimilis*, *Cranioleuca vulpina, Certhiaxis cinnamomeus*, *Certhiaxis mustelinus*, and *Tolmomyias sulphurescens insignis*. These records add to a growing body of evidence (e.g., Armacost and Capparella 2012) that these species, which we encountered in *várzea*, marshes, and in habitat surrounding oxbow lakes, have more varied habitat associations than previously thought, particularly in Brazil.

Besides its importance in evolutionary studies, the middle Juruá region is also marked by the sustainable relationship between humans and forest. Strict environmental policies in protected lands following the rubber tapper era (Ruiz-Pérez et al. 2005) reflect a rich bird fauna. We also noticed numerous populations of sensitive species that require pristine forest for survivorship. We observed high numbers of obligate army-ant followers, such as *Rhegmatorhina melanosticta*, *Hafferia fortis*, and *Phlegopsis erythroptera*; large populations of water-associated species such as the IUCN Near-threatened *Neochen jubata* (BirdLife International 2020a), *Anhima cornuta*, *Rynchops niger*, and *Phaetusa simplex*; and migratory species whose migration routes in South America are poorly understood, such as *Calidris fuscicollis*, *Calidris melanotos*, and *Tringa flavipes*. We did not observe two species of conservation concern, the vulnerable *Crax globulosa* (BirdLife International 2020b; Leite et al. 2017), and *Mitu tuberosum*, which are targets of subsistence hunting. However, local people considered these two cracids as common in the area.

Future ornithological work is necessary to improve the current knowledge of Juruá bird diversity, distributions, contact zones, and conservation status. We suggest that collecting specimens is still vitally necessary, especially in the headwaters and lower portions of the Juruá that encompass a variety of natural laboratories for the study of Amazonian bird speciation.

Acknowledgments The data presented here are the results of the Emilie Snethlage Expedition. This article is dedicated to Emilie Snethlage, a pioneering field ornithologist and role model for women scientists. We thank all our supporters who made this field expedition possible: Scientific Exploration Society of London, Coypu Foundation, LSU College of Science, the Conselho Nacional de Desenvolvimento Científico e Tecnológico do Brasil (CNPq), Sir Charles Blois, Thomas and Melissa Wafer, Robb Brumfield, Mike Harvey, Brant Faircloth, Nikki Skinner, Tatiana Pongiluppi, Thiago Vernaschi Vieira da Costa, Gabriel Leite, Andressa Scabin, Tammie Jackson, Valerie Derouen, Mario Cohn-Haft, Luciano Naka, Camila Ribas, Erika Zingst-Zaher, Carlos Pitaluga, Jessica Manafi, and Dawn Jenkins. We thank Robb Brumfield, Dan Lane, Van Remsen, Oscar Johnson, Andre Moncrieff, and an anonymous reviewer for their valuable comments on the manuscript. We thank Ilse Grantsau and Ingo Grantsau for providing the abstract in German. We thank Angela Prochilo for the help along fieldwork and for documenting our expedition in a video documentary. We are grateful for the help and support provided by the managers of Reserva do Desenvolvimento Sustentável Uacari, and Reserva Extrativista do Médio Juruá. We are grateful to the community leaders who allowed us to work in their lands, and to our local field guides Almir Rogério Nascimento, Ana Lucia Teixeira da Silva, and Josué Campello Cavalcante. Fieldwork complied with the current laws of Brazil, and it was undertaken under SISBIO permit: 28294-14, CONCEA permit, and LSU IACUC Protocol 18-054.

Author contributions GDR conceived the article idea. GDR, MJM, BC, AEH, GL, BM, JFS, MAR, and DCS collected data in the field. GDR, MJM, BC, AEH, GL, BM, JFS, LFS, MAR, and DCS curated the data, and performed analysis. GDR, MJM, BC, AEH, GL, BM, JFS, LFS, MAR, and DCS wrote and edited the manuscript.

Funding Fieldwork was funded by the Scientific Exploration Society of London, the Coypu Foundation, the LSU College of Science, the Conselho Nacional de Desenvolvimento Científico e Tecnológico do Brasil (CNPq), Sir Charles Blois, and Thomas and Melissa Wafer.

Data availability The data collected along fieldwork are available in details in Tables S1 and S2.

Compliance with ethical standards

Conflict of interest There is no conflict of interest for all authors.

Ethical approval Fieldwork was undertaken under permit of the Brazilian Animal Ethics Committee (CONCEA) and LSU IACUC Protocol 18-054.

Informed consent All the authors declare consent for publication.

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