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The Amazon River as a dispersal barrier to passerine birds: effects of river width, habitat and taxonomy

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ABSTRACT

Aim To evaluate the relative effectiveness of the lower and upper sections, respectively, of the Amazon River as a barrier to bird distribution, and to evaluate ecological and taxonomic factors affecting the efficacy of the river barrier.

Location Amazon River of South America between its confluence with the Napo River in the west and its delta in the east.

Methods Using published distribution maps for 448 species of passerine birds occurring along the Amazon River, we evaluated whether each was distributed along one bank only (river presumed to be a barrier) or both banks (no barrier) to test the predictions that the river was more effective as a dispersal barrier: (1) along the lower, wider portion of the river than the upper, narrower portion; (2) for species inhabiting forests than open country; (3) for species inhabiting forest understorey than forest canopy; (4) for species restricted to *terra firme* (never inundated upland forest) than those not restricted to *terra firme* and (5) for certain taxonomic groups.

Results Our analyses demonstrated that the Amazon River was most effective as a dispersal barrier along its lower portion and for species restricted to forests and *terra firme*. However, the river was not significantly more of a barrier for species inhabiting forest understorey than forest canopy. The river was most significant as a barrier to dispersal for the antbirds (Thamnophilidae) and was less significant as a barrier to species belonging to several large families including woodcreepers (Dendrocolaptidae), ovenbirds (Furnariidae), flycatchers (Tyrannidae), cotingids (Cotingidae), tanagers (Thraupidae), seed-eating finches (Emberizidae) and blackbirds (Icteridae).

Main conclusions The robust widths of Amazonian rivers are widely considered to represent impediments to dispersal and gene flow for many taxa of birds and other animals, and may have represented agents of vicariance in the diversification of species. Our study reaffirms the effectiveness of the lower Amazon River as a current barrier to bird dispersal for forest birds and provides new insights into the effects of habitat and taxonomy on the efficacy of the river barrier. Although supportive of several predictions of the river hypothesis of biological diversification, our study is limited in addressing the historical impact of river barriers as agents of vicariance in the process of diversification.

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INTRODUCTION

A plethora of hypotheses have been postulated to explain the extraordinary diversification of birds in the tropical forests of South America, which host the most diverse bird faunas in the world (e.g. see recent reviews by Haffer, 1997a; Nores, 2000). The extent to which of these hypotheses best accounts for the immense diversification of the Neotropical avifauna remains the subject of intense debate. One such hypothesis, generally referred to as the 'river hypothesis' or 'riverine barrier hypothesis', postulates that the formation of large Amazonian rivers, due to uplifting of the Andes *c*. 5 Ma (Hoorn *et al.*, 1995; Campbell *et al.*, 2001), fragmented formerly contiguous bird populations into isolated units where differentiation occurred and continues to occur in allopatry (e.g. Sick, 1967; Haffer, 1974; Capparella, 1988, 1991).

As noted by early naturalist explorers (e.g. Wallace, 1852, 1876; Bates, 1863), the robust widths of Amazonian rivers, representing the largest river system in the world, delimit the ranges of many taxa of birds and other organisms, and potentially pose an impediment to dispersal. In birds, many pairs of presumed sister taxa are separated by Amazonian rivers (e.g. see maps in Haffer, 1974, 1978, 1985, 1987; Ridgely & Tudor, 1989, 1994). This pattern is unique to the Amazon River. For example, South America's second largest river system, the Paraguay–Paraná system, does not pose a significant barrier to bird dispersal (Hayes, 1995). Capparella (1988, 1991) provided evidence for genetic differentiation between phenotypically similar and dissimilar taxa separated by the Amazon River, thus demonstrating the Amazon River's potential effectiveness as an impediment to gene flow among bird taxa.

The effectiveness of Amazonian rivers as barriers to dispersal is generally thought to be greatest along the lower, wider portions of the river, where the river presents a greater obstacle than where it narrows upstream (e.g. Haffer, 1974). Sick (1967) and Capparella (1988, 1991) predicted that birds inhabiting the dark understorey would be the least likely to cross large light gaps such as rivers, in contrast with species inhabiting the forest canopy and open country which presumably are more accustomed to light gaps. They also predicted that the barrier effect would be greater for species restricted to *terra firme* forest (never inundated upland forest), for which the effective distance across the river is greater than that between the periodically inundated lowland *várzea* forest along river banks. However, these hypotheses have not been rigorously tested across a broad spectrum of avian taxa.

In this paper we analyse the distribution of passerine birds along the Amazon River to empirically test the following predictions: (1) the lower, wider portion of the river is a greater barrier to dispersal than the upper, narrower portion; (2) the river is a greater barrier for species inhabiting forests than open country; (3) the river is a greater barrier for species inhabiting forest understorey than forest canopy; (4) the river is a greater barrier for species restricted to *terra firme* forest than those not restricted to *terra firme* (often occurring in the intervening *várzea* forest) and (5) the effectiveness of the river

as a barrier varies among taxonomic groups. Although this approach tests several predictions of the river hypothesis of biological diversification, it assesses only the current nature of the Amazon River as a dispersal barrier and is limited in addressing the historical impact of river barriers as agents of vicariance in the process of diversification.

METHODS

We divided the course of the Amazon River into two sections. The upper, narrower section extended from the confluence of the Napo River to the confluence of the Negro River (in Manaus); the lower, wider section extended from the junction of the Negro River to the delta where it meets the Atlantic Ocean (Fig. 1). Data on the distribution of passerine birds (order Passeriformes) were obtained from the most accurately prepared distributional range maps available for the Amazon region (Ridgely & Tudor, 1989, 1994); similarly accurate distributional range maps are not yet available for non-passerine species. Our analysis was limited to those species whose range was illustrated as virtually touching the Amazon

Figure 1 Map of South America illustrating the geographical extent of the Amazon River system and the two sections used in this study: the upper, narrower section from points A-B and the lower, wider section from points B-C.

River in a map. We considered a section of the river to pose a dispersal barrier if the species was distributed along one bank but not the other; if the species occurred on both sides of the river, we considered the river not to pose a dispersal barrier.

Based on the preferred habitat descriptions in Ridgely & Tudor (1989, 1994), each species of passerine bird (introduced species excluded) was classified as belonging to one of three different habitat categories. Forest understorey species inhabited the lower and middle levels (rarely in canopy) of forest interior, although sometimes occurring at forest edges, of any type of forest. Forest canopy species inhabited the middle to upper levels (rarely in understorey) of forest interior and forest edges of any type of forest. Open country species generally occurred outside of the forest such as at forest edges, early secondary growth, savannas, and sand bars, but also included habitat generalists occurring within the interior of forests as well. Species whose habitat was unknown were excluded from the habitat analyses. We also classified each species as either restricted to *terra firme* forest (never inundated upland forest) or not restricted to *terra firme*, including *várzea* (periodically inundated lowland vegetation along river banks, sometimes discontinuously); the latter category was used for species inhabiting both *várzea* and *terra firme*. To examine potential differences among taxonomic groups, the data collected (see Appendix) were pooled within taxonomic families (based on South American Checklist Committee, unpublished draft, April 2004).

Two-sample chi-square tests (χ^2 value, including Yates's correction for continuity in two-by-two contingency tables) or Fisher exact probability tests (depending on sample size; Zar, 1984) were used to compare the proportions of species belonging to different river sections, habitat, or taxonomic categories for which the river posed a potential dispersal barrier. All statistical tests were computed with Statistix 7.0 software (Anonymous, 2000).

RESULTS

River width

For all passerine bird species combined ($n = 448$), the lower, wider section of the Amazon River was a significantly greater barrier to bird dispersal (19.8%, $n = 400$) than the upper, narrower section (8.3%, $n = 337$; $\chi^2 = 18.38$, d.f. = 1, $P < 0.001$; Table 1). Further effects of river width on bird species distribution within different habitat and taxonomic categories are summarized below.

Habitat

The habitat was unknown for three species of birds excluded from the analyses of habitat. Of 397 species of passerine birds occurring along the lower section of the Amazon River, the river posed a significantly greater barrier to dispersal for forest understorey species (29.4%, $n = 170$) and forest canopy species (24.7%, $n = 93$) than for open country species (4.5%,

Table 1 Number of species in passerine families for which the Amazon River formed or did not form a dispersal barrier along two sections of the Amazon River

Family	Lower section		Upper section		
	Barrier	Non-barrier	Barrier	Non-barrier	χ^2
Dendrocolaptidae	4	20	1	21	0.71
Furnariidae	4	27	0	29	2.20
Thamnophilidae	28	40	9	52	9.72*
Formicariidae	2	6	2	6	NS†
Conopophagidae	1	0	0	0	–
Rhinocryptidae	1	0	0	1	NS†
Tyrannidae	11	78	3	71	2.57
Cotingidae	5	22	0	21	2.58
Pipridae	11	9	3	9	1.66
Vireonidae	1	8	0	7	NS†
Corvidae	1	0	0	1	NS†
Hirundinidae	0	6	0	6	NS†
Troglodytidae	3	6	1	8	NS†
Polioptilidae	1	3	1	2	NS†
Turdidae	0	6	0	5	NS†
Mimidae	0	1	0	0	–
Motacillidae	0	1	0	0	–
Coerebidae	0	1	0	0	–
Thraupidae	2	35	4	34	0.15
Emberizidae	1	19	1	10	0.00
Cardinalidae	0	6	0	4	–
Parulidae	0	3	0	0	–
Icteridae	1	18	2	16	0.00
Fringillidae	2	6	1	6	NS†
Totals	79	321	28	309	

*$P < 0.01$.

†Non-significant (Fisher exact $P > 0.05$).

$n = 134$; $\chi^2 = 31.01$, d.f. = 2, $P < 0.001$; Table 2). The lower section was a significantly greater barrier for all forest birds combined ($\chi^2 = 28.74$, d.f. = 1, $P < 0.001$). However, the river was no more of a barrier for forest understorey than forest canopy species ($\chi^2 = 0.44$, d.f. = 1, $P = 0.51$). In contrast with the lower section, the upper section of the Amazon River posed no more of a dispersal barrier for birds (335 species) of any habitat category (forest understorey, 9.7%, $n = 155$; forest canopy, 7.3%, $n = 82$; open country, 7.1%, $n = 98$; $\chi^2 = 0.66$, d.f. = 2, $P = 0.72$; Table 2). The lower section was a greater dispersal barrier than the upper section for forest understorey species ($\chi^2 = 18.52$, d.f. = 1, $P < 0.001$) and forest canopy species ($\chi^2 = 8.34$, d.f. = 1, $P < 0.001$), but not for open country species ($\chi^2 = 0.34$, d.f. = 1, $P = 0.56$).

The lower section of the river formed a significantly greater dispersal barrier for passerine bird species restricted to *terra firme* (37.7%, $n = 43$) than for those not restricted to *terra firme* (16.2%, $n = 328$; $\chi^2 = 15.24$, d.f. = 1, $P < 0.001$; Table 3). The upper section appeared to be a greater barrier for species restricted to *terra firme* (14.9%, $n = 67$) than those not restricted to terra firme (6.7%, $n = 268$), but the differences

Table 2 Number of species in passerine families for which the Amazon River formed/did not form a dispersal barrier along two sections of the Amazon River in different habitats

Family	Lower section			Upper section		
	FU	FC	OC	FU	FC	OC
Dendrocolaptidae*	2/13	2/5	0/1	0/14	1/6	0/0
Furnariidae*	0/15	4/2	0/9	0/15	0/6	0/8
Thamnophilidae*	24/30	4/7	0/2	6/43	2/6	1/2
Formicariidae	2/6	0/0	0/0	2/6	0/0	0/0
Conopophagidae	1/0	0/0	0/0	0/0	0/0	0/0
Rhinocryptidae	1/0	0/0	0/0	0/1	0/0	0/0
Tyrannidae	3/24	5/16	3/38	1/27	1/19	1/25
Cotingidae	2/6	3/9	0/7	0/6	0/9	0/6
Pipridae	11/8	0/1	0/0	3/8	0/1	0/0
Vireonidae	0/1	1/5	0/2	0/1	0/5	0/1
Corvidae	0/0	0/0	1/0	0/0	0/0	0/1
Hirundinidae	0/0	0/0	0/6	0/0	0/0	0/6
Troglodytidae	3/3	0/0	0/3	1/5	0/0	0/3
Polioptilidae	1/1	0/1	0/1	1/1	0/0	0/1
Turdidae	0/3	0/0	0/3	0/4	0/0	0/1
Mimidae	0/0	0/0	0/1	0/0	0/0	0/0
Motacillidae	0/0	0/0	0/1	0/0	0/0	0/0
Coerebidae	0/0	0/0	0/1	0/0	0/0	0/0
Thraupidae	0/4	2/16	0/15	1/4	2/16	1/14
Emberizidae	0/1	0/0	1/18	0/1	0/0	1/8
Cardinalidae	0/3	0/1	0/2	0/2	0/1	0/2
Parulidae	0/1	0/1	0/1	0/0	0/0	0/0
Icteridae	0/1	0/3	1/14	0/1	0/4	2/11
Fringillidae	0/0	2/3	0/3	0/1	0/3	1/2
Totals	50/120	23/70	6/128	15/140	6/76	7/91

*One species for which habitat was unknown.
FU, forest understorey; FC, forest canopy; OC, open country.

Table 3 Number of species in passerine families for which the Amazon River formed/did not form a dispersal barrier along two sections of the Amazon River

Family	Lower section		Upper section	
	TF	NTF	TF	NTF
Dendrocolaptidae*	2/8	2/11	1/9	0/11
Furnariidae*	2/8	2/18	0/10	0/19
Thamnophilidae*	15/13	13/26	6/23	3/28
Formicariidae	1/4	1/2	2/4	0/2
Rhinocryptidae	1/0	0/0	0/1	0/0
Conopophagidae	1/0	0/0	0/0	0/0
Tyrannidae	0/7	11/71	0/7	3/64
Cotingidae	0/1	5/21	0/1	0/20
Pipridae	2/0	9/9	0/1	3/8
Vireonidae	1/1	0/7	0/1	0/6
Corvidae	0/0	1/0	0/0	0/1
Hirundinidae	0/0	0/6	0/0	0/6
Troglodytidae	0/0	3/6	0/0	1/8
Polioptilidae	1/0	0/3	1/0	0/2
Turdidae	0/0	0/6	0/0	0/5
Mimidae	0/0	0/1	0/0	0/0
Motacillidae	0/0	0/1	0/0	0/0
Coerebidae	0/0	0/1	0/0	0/0
Thraupidae	0/1	2/34	0/0	4/34
Emberizidae	0/0	1/19	0/0	1/9
Cardinalidae	0/0	0/6	0/0	0/5
Parulidae	0/0	0/3	0/0	0/0
Icteridae	0/0	1/18	0/0	2/16
Fringillidae	0/0	2/6	0/0	1/6
Totals	26/43	53/275	10/57	18/250

*One species for which habitat was unknown
TF, restricted to *terra firme*; NTF, not restricted to *terra firme*.

were not quite significant ($\chi^2 = 3.70$, d.f. = 1, $P = 0.054$; Table 3). The lower section was a greater dispersal barrier than the upper section for species restricted to *terra firme* ($\chi^2 = 7.91$, d.f. = 1, $P < 0.005$) and also for those not restricted to *terra firme* ($\chi^2 = 11.65$, d.f. = 1, $P < 0.001$). For species restricted to *terra firme*, the Amazon River did not form a significantly greater barrier for forest understorey species (42.9%, $n = 49$ in lower section; 17.0%, $n = 47$ in upper section) than for forest canopy species (26.3%, $n = 19$ in lower section; 7.1%, $n = 15$ in upper section) in either the lower section ($\chi^2 = 0.48$, d.f. = 1, $P = 0.49$) or upper section ($\chi^2 = 0.33$, d.f. = 1, $P = 0.57$; Table 4).

Among forest understorey species, the lower section of the Amazon River formed a significantly greater barrier for species restricted to *terra firme* (42.9%, $n = 49$) than for those not restricted to *terra firme* (24.0%, $n = 121$; $\chi^2 = 5.12$, d.f. = 1, $P = 0.02$); however, the upper Amazon River was not quite a significantly greater barrier for species restricted to *terra firme* (17.0%, $n = 47$) than for those not restricted to *terra firme* (6.9%, $n = 108$; $\chi^2 = 3.04$, d.f. = 1, $P = 0.08$; Table 4). The lower section of the river formed a significantly greater barrier than the upper section for forest understorey species restricted

Table 4 Number of species in different habitat groups for which the Amazon River formed/did not form a dispersal barrier along two sections of the Amazon River

	Lower section		Upper section	
	TF	NTF	TF	NTF
Forest understorey	21/28	29/92	8/39	7/101
Forest canopy	5/12	18/58	1/14	5/62

TF, restricted to *terra firme*; NTF, not restricted to *terra firme*.

to *terra firme* ($\chi^2 = 6.42$, d.f. = 1, $P = 0.01$) and also for forest understorey species not restricted to *terra firme* ($\chi^2 = 11.88$, d.f. = 1, $P < 0.001$).

For forest canopy species, neither section of the river formed a significantly greater barrier for species restricted to *terra firme* (26.3%, $n = 19$ for lower; 7.1%, $n = 15$ for upper) than for those not restricted to *terra firme* (23.7%, $n = 58$ for lower; 13.4%, $n = 67$ for upper; $\chi^2 = 0.03$, d.f. = 1, $P = 0.85$ for lower; $\chi^2 = 0.0$, d.f. = 1, $P = 1.00$ for upper; Table 4). The lower section of the river did not form a significantly greater barrier than the upper section for forest canopy species

restricted to *terra firme* ($\chi^2 = 1.42$, d.f. = 1, $P = 0.23$); in contrast, the lower section formed a greater barrier than the upper section for forest canopy species not restricted to *terra firme* ($\chi^2 = 5.79$, d.f. = 1, $P = 0.02$).

Taxonomy

Antbirds of family Thamnophilidae were the only one of 24 bird families in which the lower section of the river represented a significantly greater barrier than the upper section (Table 1). Although many families were represented by few species, thus limiting the efficacy of statistical tests, most species belonging to several large families were apparently less affected by the river as a dispersal barrier, including the woodcreepers (Dendrocolaptidae), ovenbirds (Furnariidae), flycatchers (Tyrannidae), cotingas (Cotingidae), tanagers (Thraupidae), seed-eating finches (Emberizidae) and blackbirds (Icteridae).

Within the family Thamnophilidae, the river formed a barrier for 43.4% of forest understorey species ($n = 53$) in the lower section but only 12.2% of forest understorey species ($n = 49$) in the upper section ($\chi^2 = 10.66$, d.f. = 1, $P = 0.001$; Table 2), and for 53.6% of species ($n = 28$) restricted to *terra firme* in the lower section but only 20.7% of such species ($n = 29$) in the upper section ($\chi^2 = 5.28$, d.f. = 1, $P = 0.02$; Table 3). Among forest understorey species, the lower section of the river was a significantly greater barrier for those restricted to *terra firme* (62.5%, $n = 24$) than for those not restricted to *terra firme* ($\chi^2 = 5.17$, d.f. = 1, $P = 0.02$); however, the upper section was no more of a barrier for those restricted to *terra firme* (20.0%, $n = 25$) than for those not restricted to *terra firme* (4.2%, $n = 24$; $\chi^2 = 1.57$, d.f. = 1, $P = 0.21$). Similar comparisons among species in forest canopy, open country, and not restricted to *terra firme* failed to find significant differences or were of limited sample size (Table 1).

Within the family Furnariidae, the lower section of the river was a greater dispersal barrier for forest canopy birds than for forest understorey and open country species ($\chi^2 = 18.46$, d.f. = 2, $P < 0.001$), but there were no significant differences in the effectiveness of the river barrier between lower and upper sections of the river ($P > 0.05$; Table 1). The river was a barrier to 57.9% of forest understorey manakins of the family Pipridae ($n = 19$ species) in the lower section in contrast with 27.3% ($n = 11$ species) in the upper section, but the differences were not significant ($\chi^2 = 1.54$, d.f. = 1, $P = 0.21$; Table 1). Similar analyses within other taxonomic groups failed to find any significant comparisons, but sample sizes were too small for most comparisons.

DISCUSSION

As with all scientific research, the validity of our conclusions is premised upon the accuracy of our data. We recognize that much has been learned regarding the taxonomy, distribution and habitat use of Amazonian birds since the publications of Ridgely & Tudor (1989, 1994), and that much remains to be learned. Although some revision of our taxonomic, distributional and habitat use categories undoubtedly would be needed as new data are acquired, we believe the data presented in Ridgely & Tudor (1989, 1994) remain adequate for accurately testing our hypotheses and that such revision would not significantly alter our conclusions. Another limitation of our data is that species are treated as independent units but instead are linked through phylogenetic relationships. Our separate comparisons of species within families attempt to address the potential effects of taxonomy on distribution.

As for our interpretations of whether or not the river represented a barrier for each species, our operational definitions (range on only one bank within a section representing a barrier; range on both banks representing no barrier) appeared adequate in most cases but may not have been for others. The distributions of some species barely reached one bank of the Amazon, in which case the river may not have been a barrier although we scored it as such. In other cases the range of a species was delimited by the river along a substantial portion of a particular segment yet crossed the river near the upstream end of the section, suggesting that the river may have been a barrier downstream but was not scored as such. A few species were confined primarily to one bank with one or a few records on the opposing back, yet were scored as the river not being a barrier when indeed it may have been an effective, though not impermeable, barrier. While recognizing the limitations of our definitions for what constitutes a river barrier, we believe the broad support found for our predictions affirms the usefulness of our definitions.

Our analyses strongly support the prediction that the lower, wider section of the Amazon River is a greater barrier to dispersal for passerine birds than the upper, narrower section. Haffer (1978, p. 71) and Beven *et al.* (1984, p. 388) plotted the number of bird species whose distribution was bordered by the river in Amazonia and demonstrated that the lower Amazon River and its larger tributaries delimit the distribution of more bird species than the upper Amazon and its tributaries. Ayres & Clutton-Brock (1992) demonstrated that primate faunas on opposite banks of Amazonian rivers were most dissimilar along the lower, wider rivers and became more similar farther upstream, indicating that the barrier effect is similar for primates; however, rivers apparently do not pose a significant barrier to the genus *Ateles* (Collins & Dubach, 2000). Obviously the river ceases to be a barrier as it becomes narrower upstream, where it is often crossed by bird species whose ranges are delimited by the lower Amazon River and its larger tributaries.

The Amazon River is clearly more of a barrier to forest birds than open country species, as predicted, illustrating the apparent reluctance of many forest-dwelling species to leave their familiar environs and stray across wide rivers. Somewhat surprisingly, our analyses revealed that the river is only marginally but not significantly a greater barrier for species inhabiting the forest understorey than for those in the forest canopy. Forest understorey species are accustomed to low

levels of light within the forest whereas forest canopy species are presumably more accustomed to more light and might be more predisposed to crossing a large light gap (Sick, 1967; Capparella, 1988, 1991). Remsen & Parker (1983) pointed out that many species of forest understorey birds thought to be relatively poor dispersers, including the Undulated Tinamou (*Crypturellus undulatus*), are adapted to inhabiting river-created habitats and readily cross large expanses of rivers to colonize islands on a seasonal basis. The often-repeated assertion that forest understorey birds are especially affected by river barriers appears to be overstated.

As the distance between *terra firme* forest on opposite banks of the river is greater than the distance between *várzea* forest bordering river banks, it comes as no surprise that the barrier effect is enhanced for species restricted to *terra firme* forest. Remsen & Parker (1983) pointed out that roughly 15% of the non-aquatic bird species resident in Amazonia are restricted to habitats created by rivers, such as beaches and sandbars, river edge forest, *várzea* forest, transitional forest and water edge. Such specialization is unique to the Amazon. For these species large rivers are less likely to pose a barrier to dispersal.

Taxonomic differences in the effectiveness of the river as a dispersal barrier may be related to differences in dispersal abilities, morphology (e.g. body size), habitat use, diet or migratory status. Although we have not attempted a rigorous assessment of the effects of these factors on bird distribution in Amazonia, a few patterns merit discussion. Large rivers obviously do not pose a barrier for aerial insectivores such as swallows and martins (Hirundinidae), which typically forage over grasslands and large expanses of water. Several large families (Cotingidae, Thraupidae and Emberizidae) and a few smaller ones (Vireonidae, Turdidae, Mimidae, Cardinalidae and Fringillidae) are comprised chiefly of species that forage on fruits and seeds, which often occur in open or edge habitats and may be seasonal in their availability; large rivers do not appear to represent a dispersal barrier for most of these species. However, rivers apparently represent a formidable barrier for many species of manakins (Pipridae), which are primarily frugivorous but usually occur within forests. The family most affected by river barriers (Thamnophilidae) is represented primarily by insectivorous species, but rivers apparently pose a less significant barrier for species belonging to three other large families of predominantly insectivorous species (Dendrocolaptidae, Furnariidae and Tyrannidae). The reason(s) why one taxonomic group would be more sensitive to river barriers than all others remains obscure.

The potential role of Amazonian rivers in generating biodiversity continues to be debated. Mayr (1942, p. 228) explicitly hypothesized that Amazonian rivers had 'initiated the first steps of speciation.' Sick (1967, p. 517) discussed the 'vicarious forms (geographical races)' of birds 'on the opposite banks of certain rivers' and postulated that the ancestors of Amazonian birds 'lived at a time when the area was not yet divided by large rivers as it is today'.

Capparella (1988, 1991) provided evidence of genetic differentiation between river-divided populations of at least five monotypic species lacking phenotypic differentiation and between three pairs of closely related, phenotypically differentiated taxa whose ranges are delimited by Amazonian rivers, thus demonstrating the Amazon River's potential effectiveness as an impediment to gene flow among bird taxa. A series of studies along the Juruá River, including analyses of genetic and morphological variation of frogs (Gascon *et al.*, 1996, 1998; Lougheed *et al.*, 1999), genetic diversity of a spiny rat (Patton *et al.*, 1994), and community composition of amphibians and small mammals (Gascon, 1996; Gascon *et al.*, 2000), failed to support predictions of the river hypothesis. However, as pointed out by Haffer (1997a, p. 460), the Juruá River is a tributary of the Amazon River located far upstream where it 'hardly represents a barrier'. An analysis of genetic variation within a mosquito failed to find evidence of a river barrier across the Amazon's delta (Fairley *et al.*, 2002).

In a series of papers on the biogeography of Amazonian birds, Haffer (1974, 1978, 1982, 1985, 1987, 1990, 1992a,b, 1993, 1997a,b; Haffer & Fitzpatrick, 1985; Haffer & Sick, 1993; Haffer & Prance, 2001) regarded the lowermost portions of the Amazon and its largest tributaries as effective barriers to bird dispersal but repeatedly discredited the role of such barriers as agents of vicariance, favouring instead a 'refuge hypothesis' for which considerable evidence was marshalled. Haffer mustered several arguments against the effectiveness of rivers as agents of vicariance: (1) the rivers and forests developed together as an interrelated process rather than separately; (2) the rivers were narrower during drier glacial periods; (3) the ranges of many species are not delimited by the river; (4) contact zones between presumed sister taxa often do not coincide with rivers; (5) many species whose ranges are delimited by the river do not have a taxonomic replacement on the opposing bank; (6) meandering loops of the river often cut off portions of land and transport their faunas to the opposite bank and (7) many species circumvent large rivers or hybridise with presumed sister taxa farther upstream. Haffer questioned the effectiveness of even the largest rivers in genetically isolating populations, initially suggesting that the effect of river barriers 'may be restricted to variation at the subspecies level' (Haffer, 1969, p. 136) and contending that 'in many cases interspecific competition rather than inability to cross the watercourse determines species range borders to coincide with a river in Amazonia' (Haffer, 1978, p. 70), but later conceding that 'some birds and other vertebrates may have originated in central Amazonia through geographical isolation of ancestral populations by rivers alone' (Haffer, 1997b, p. 299).

Our study reaffirms the effectiveness of the lower Amazon River as a current barrier to bird dispersal for forest birds and provides new insights into the effects of habitat and taxonomy on the efficacy of the river barrier. Although supportive of several predictions of the river hypothesis of biological diversification, our study is limited in addressing the historical impact of river barriers as agents of vicariance in the process of diversification. Further studies of palaeoecology, population genetics and phylogeography of many

more taxa are needed to better assess the role of Amazonian river barriers in generating biodiversity.

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BIOSKETCHES

Prior to his current job as an associate professor, **Floyd Hayes** worked for a year as a wildlife biologist in the US Virgin Islands, taught biology in two tertiary institutions in Trinidad for 9 years and worked as a biologist for the US Peace Corps in Paraguay for 3 years. His research focuses on the distribution, biogeography, ecology and behaviour of Neotropical birds.

Jo-Anne N. Sewlal is currently studying the ecology of *Mesabolivar aurantiacus*, an attractive red pholcid spider commonly inhabiting the semi-open spaces of buttresses of rain forest trees, for her MPhil degree in zoology at the University of the West Indies in Trinidad.

APPENDIX

Habitat, forest type and barrier effects of the Amazon River on passerine bird species. Habitat: FU = forest understorey; FC = forest canopy; O = open country; ? = unknown. Forest type: * = *terra firme*. Barrier effect (lower river/upper river): B = river a barrier; N = river not a barrier; – = absent in section. Habitat and barrier data based on Ridgely & Tudor (1989, 1994). Taxonomy based on South American Checklist Committee (unpubl. draft, April 2004), with two exceptions based on Ridgely & Tudor (1989, 1994) and the placement of two 'incertae sedis' taxa noted in brackets.

DENDROCOLAPTIDAE: *Dendrocincla fuliginosa*, FU, N/N; *D. merula*, FU*, N/N; *Deconychura longicauda*, FU*, N/N; *D. stictolaema*, FU*, N/N; *Sittasomus griseicapillus*, FC, N/N; *Glyphorynchus spirurus*, FU*, N/N; *Nasica longirostris*, FC, N/N; *Dendrexetastes rufigula*, FC, N/N; *Hylexetastes stresemanni*, FC, -/N ; *H. uniformis*, FC*, B/B [herein treated as distinct from following species]; *H. perrotii*, FC*, B/-; *Xiphocolaptes promeropirhynchus*, FU, N/N; *Dendrocolaptes certhia*, FU, N/N; *D. picumnus*, FU*, N/N; *Xiphorhynchus picus*, FU, N/N; *X. kienerii*, ?, N/N; *X. obsoletus*, FU, N/N; *X. ocellatus*, FU*, N/N; *X. spixii*, FU, B/N; *X. pardalotus*, FU, B/N; *X. guttatus*, FC, N/N; *Lepidocolaptes angustirostris*, O, N/-; *L. albolineatus*, FC*, N/N; *Campylorhamphus trochilirostris*, FU, N/N; *C. procurvoides*, FU*, N/N.

FURNARIIDAE: *Furnarius figulus*, O, N/-; *F. leucopus*, O, N/N; *F. torridus*, O, -/N; *F. minor*, O, N/N; *Synallaxis albescens*, O, N/N; *S. albigularis*, O, N/N; *S. hypospodia*, O, N/B; *S. rutilans*, FU, N/N; *S. propinqua*, FU, N/N; *S. gujanensis*, FU, N/N; *Cranioleuca vulpina*, FU, N/N; *C. gutturata*, FU, N/N; *C. muelleri*, ?, N/B; *Certhiaxis cinnamomeus*, O, N/N; *C. mustelinus*, O, N/N; *Thripophaga fusciceps*, FU, N/-; *Metopothrix aurantiaca*, FC, -/N; *Berlepschia rikeri*, O, N/N; *Ancistrops strigilatus*, FC*, B/N; *Hyloctistes subulatus*, FU, -/N; *Philydor ruficaudatum*, FC*, N/N; *P. erythrocercum*, FU*, N/N; *P. erythropterum*, FC*, B/N; *P. pyrrhodes*, FU, N/N; *Automolus ochrolaemus*, FU*, N/N; *A. infuscatus*, FU*, N/N; *A. rubiginosus*, FU*, -/N; *A. rufipileatus*, FU, N/N; *Sclerurus mexicanus*, FU*, N/-; *S. rufigularis*, FU*, N/N; *S. caudacutus*, FU*, N/N; *Xenops milleri*, FC*, N/N; *X. tenuirostris*, FC, B/N; *X. minutus*, FU, N/N; *X. rutilans*, FC, B/-.

THAMNOPHILIDAE: *Cymbilaimus lineatus*, O, N/N; *Frederickena viridis*, FU, B/-; *F. unduligera*, FU*, -/N; *Taraba major*, FU, N/N; *Sakesphorus canadensis*, O, -/B; *S. luctuosus*, FU, N/-; *Thamnophilus doliatus*, FU, N/N; *T. nigrocinereus*, FU, N/-; *T. cryptoleucus*, FU, -/N; *T. aethiops*, FU*, B/N; *T. schistaceus*, FU*, B/N; *T. murinus*, FU, N/N; *T. punctatus*, FU*, N/-; *T. amazonicus*, FU, N/N; *Megastictus margaritatus*, FU*, -/N; *Neoctantes niger*, FU, -/N; *Thamnomanes ardesiacus*, FU*, B/N; *T. saturninus*, FU*, B/B; *T. caesius*, FU*, N/N; *T. schistogynus*, FU, -/B; *Pygiptila stellaris*, FC, B/N; *Myrmotherula gutturalis*, FU, B/-; *M. leucophthalma*, FU, B/-; *M. haematonota*, FU*, N/N; *M. ornata*, FU, B/-; *M. erythrura*, FU*, N/N; *M. brachyura*, FC, N/N; *M. ignota*, FC, -/N; *M. sclateri*, FC, B/B; *M. surinamensis*, O, N/N; *M. klagesi*, FC, N/-; *M. hauxwelli*, FU, B/N; *M. guttata*, FU*, B/-; *M. axillaris*, FU, N/N; *M. longipennis*, FU*, N/N; *M. iheringi*, FU, B/-; *M. menetriesii*, FC*, N/N; *M. assimilis*, ?, N/N; *Dichrozona cincta*, FU*, B/N; *Herpsilochmus dugandi*, FC*, -/B; *H. dorsimaculatus*, FC, B/-; *H. rufimarginatus*, FC, B/-; *Microrhopias quixensis*, FU, N/N; *Formicivora grisea*, FU, N/-; *Terenura humeralis*, FC*, N/N; *T. spodioptila*, FC*, N/-; *Cercomacra cinerascens*, FC*,

N/N; *C. nigrescens*, FU, N/N; *C. serva*, FU, -/N; *Pyriglena leuconota*, FU, B/-; *Myrmoborus leucophrys*, FU, N/N; *M. lugubris*, FU, N/N; *M. myotherinus*, FU*, B/N; *Hypocnemis cantator*, FU, N/N; *H. hypoxantha*, FU*, B/N; *Hypocnemoides melanopogon*, FU, N/N; *H. maculicauda*, FU*, B/B; *Myrmochanes hemileucus*, FU, N/N; *Sclateria naevia*, FU, N/N; *Percnostola rufifrons*, FU, B/N; *Schistocichla schistacea*, FU*, -/N; *S. leucostigma*, FU*, N/N; *Myrmeciza longipes*, FU, B/-; *M. hemimelaena*, FU*, B/N; *M. atrothorax*, FU, N/N; *M. melanoceps*, FU, -/N; *M. hyperythra*, FU, -/N; *M. fortis*, FU*, -/N; *M. torquata*, FU, N/-; *Pithys albifrons*, FU*, B/B; *Gymnopithys leucaspis*, FU*, -/B; *G. rufigula*, FU*, B/-; *G. salvini*, FU, B/B; *Rhegmatorhina gymnops*, FU*, B/-; *R. berlepschi*, FU*, B/-; *R. melanosticta*, FU*, -/N; *Hylophylax naevia*, FU*, N/N; *H. punctulatus*, FU, N/N; *H. poecilinotus*, FU*, N/N; *Phlegopsis erythroptera*, FU*, -/N.

FORMICARIIDAE: *Formicarius colma*, FU*, N/N; *F. analis*, FU, N/N; *Chamaeza nobilis*, FU*, B/N; *Grallaria varia*, FU*, N/B; *Hylopezus macularius*, FU* N/N; *H. berlepschi*, FU, B/-; *Myrmothera campanisona*, FU, N/N.

CONOPOPHAGIDAE: *Conopophaga aurita*, FU* N/N; *C. melanogaster*, FU*, B/-; *C. peruviana*, FU*, -/B.

RHINOCRYPTIDAE: *Liosceles thoracicus*, FU*, B/N.

TYRANNIDAE: *Phyllomyias griseiceps*, O, B/-; *Tyrannulus elatus*, O, N/N; *Myiopagis gaimardii*, FC, N/N; *M. caniceps*, FC, N/N; *M. flavivertex*, FU, N/N; *M. viridicata*, FU, N/-; *Elaenia flavogaster*, O, N/B; *E. pelzelni*, FC, N/N; *E. cristata*, O, N/-; *E. chiriquensis*, O, N/N; *E. ruficeps*, O, N/-; *Ornithion inerme*, FC, N/N; *Camptostoma obsoletum*, O, N/N; *Suiriri suiriri*, O, N/-; *Serpophaga hypoleuca*, O, N/N; *Phaeomyias murina*, O, N/N; *Capsiempis flaveola*, O, N/N; *Corythopis torquata*, FU*, N/N; *Stigmatura napensis*, FU, N/N; *Zimmerius gracilipes*, FC, N/N; *Mionectes oleagineus*, FU, N/N; *M. macconnelli*, FU*, N/N; *Leptopogon amaurocephalus*, FU, -/N; *Sublegatus obscurior*, O, N/N; *Inezia subflava*, FU, N/N; *Myiornis ecaudatus*, FU, N/N; *Lophotriccus vitiosus*, FU, B/N; *L. galeatus*, FU, N/B; *Hemitriccus minor*, FU*, N/N; *H. zosterops*, FU, N/N; *H. iohannis*, FC, -/N; *H. striaticollis*, O, B/-; *H. minimus*, FC, B/-; *Poecilotriccus capitalis*, FU, -/N; *P. fumifrons*, O, N/-; *P. latirostris*, FU, B/N; *Todirostrum maculatum*, O, N/N; *T. cinereum*, O, N/-; *T. pictum*, FC, B/-; *T. chrysocrotaphum*, FC, B/-; *Cnipodectes subbrunneus*, FU, -/N; *Rhynchocyclus olivaceus*, FC, N/N; *Tolmomyias sulphurescens*, FC, N/N; *T. assimilis*, FC, N/N; *T. poliocephalus*, FC, N/N; *T. flaviventris*, FC, N/N; *Platyrinchus saturatus*, FU*, N/-; *P. coronatus*, FU, N/N; *P. platyrhynchos*, FU, N/N; *Onychorhynchus coronatus*, FU, N/N; *Myiophobus fasciatus*, O, N/N; *Myiobius barbatus*, FU, N/N; *M. atricaudus*, FU, B/-; *Terenotriccus erythrurus*, FU, N/N; *Neopipo cinnamomea*, FU, N/N; *Lathrotriccus euleri*, FU, N/N; *Cnemotriccus fuscatus*, FU, N/N; *Contopus cinereus*, O, N/-; *Knipolegus poecilocercus*, FU, N/N; *K. orenocensis*, O, N/N; *Ochthornis littoralis*, O, N/N; *Muscisaxicola fluviatilis*, O, -/N; *Xolmis cinereus*, O, N/-; *X. velatus*, O, N/-; *Fluvicola albiventer*,

O, N/-; *Arundinicola leucocephala*, O, N/N; *Legatus leucophaius*, O, N/N; *Myiozetetes similis*, O, N/N; *M. granadensis*, O, -/N; *M. luteiventris*, FC, N/N; *Pitangus sulphuratus*, O, N/N; *P. lictor*, O, N/N; *Conopias albovittatus*, FC, B/B; *C. trivirgatus*, FC, N/N; *Myiodynastes maculatus*, O, N/N; *Megarynchus pitangua*, O, N/N; *Tyrannopsis sulphurea*, O, N/N; *Empidonomus varius*, O, N/N; *E. aurantioatrocristatus*, O, B/-; *Tyrannus albogularis*, O, N/-; *T. melancholicus*, O, N/N; *T. savana*, O, N/-; *Rhytipterna simplex*, FC*, N/N; *R. immunda*, O, N/N; *Sirystes sibilator*, FC, N/N; *Casiornis fuscus*, FC, B/-; *Myiarchus tuberculifer*, FC, N/N; *M. swainsoni*, O, N/N; *M. ferox*, O, N/N; *M. tyrannulus*, O, N/-; *Ramphotrigon ruficauda*, FU, N/N; *Attila cinnamomeus*, FU, N/N; *A. citriniventris*, FC*, -/N; *A. bolivianus*, FU, N/N; *A. spadiceus*, FC*, N/N.

COTINGIDAE: *Tityra inquisitor*, O, N/N; *T. cayana*, O, N/N; *T. semifasciata*, O, N/N; *Schiffornis major*, FU, N/N; *S. turdina*, FU, N/N; *Laniocera hypopyrra*, FU, N/N; *Iodopleura isabellae*, FC, B/N; *Pachyramphus viridis*, FC, N/-; *P. rufus*, O, N/N; *P. castaneus*, O, N/N; *P. polychopterus*, O, N/N; *P. marginatus*, FC*, N/N; *P. surinamus*, O, N/-; *P. minor*, FC, N/N; *Rupicola rupicola*, FU, B/-; *Phoenicircus carnifex*, FU, N/-; *P. nigricollis*, FU, B/N; *Cotinga maynana*, FC, -/N; *C. cotinga*, FC, N/-; *C. cayana*, FC, N/N; *Lipaugus vociferans*, FU, N/N; *Porphyrolaema porphyrolaema*, FC, -/N; *Xipholena punicea*, FC, N/N; *X. lamellipennis*, FC, B/-; *Gymnoderus foetidus*, FC, N/N; *Querula purpurata*, FU, N/N; *Haematoderus militaris*, FC, N/-; *Perissocephalus tricolor*, FC, B/-; *Cephalopterus ornatus*, FC, N/N.

PIPRIDAE: *Neopelma pallescens*, FU, N/-; *N. chrysocephalum*, FU, B/-; *Tyranneutes stolzmanni*, FU, B/N; *T. virescens*, FU, B/-; *Machaeropterus regulus*, FU, -/N; *Lepidothrix coronata*, FU*, -/N; *L. nattereri*, FU*, B/-; *L. iris*, FU*, B/-; *L. serena*, FU, B/-; *Manacus manacus*, FU, N/N; *Chiroxiphia pareola*, FU, N/N; *Xenopipo atronitens*, FU, N/N; *Heterocercus linteatus*, FU, B/B; *Pipra pipra*, FU, N/N; *P. aureola*, FU, N/-; *P. filicauda*, FU, N/N; *P. erythrocephala*, FU, B/B; *P. rubrocapilla*, FU, B/B; *Piprites chloris*, FC, N/N [incertae sedis].

VIREONIDAE: *Cyclarhis gujanensis*, FC, N/N; *Vireolanius leucotis*, FC, N/N; *Vireo olivaceus*, O, N/N; *Hylophilus thoracicus*, FC, N/N; *H. semicinereus*, FC, N/N; *H. pectoralis*, O, N/-; *H. hypoxanthus*, FC*, B/N; *H. muscicapinus*, FC*, N/-; *H. ochraceiceps*, FU, N/N.

CORVIDAE: *Cyanocorax violaceus*, O, -/N; *C. cayanus*, O, B/-.

HIRUNDINIDAE: *Tachycineta albiventer*, O, N/N; *Progre tapera*, O, N/N; *P. chalybea*, O, N/N; *Pygochelidon cyanoleuca*, O, -/N; *Atticora fasciata*, O, N/N; *Neochelidon tibialis*, O, N/-; *Stelgidopteryx ruficollis*, O, N/N.

TROGLODYTIDAE: *Campylorhynchus turdinus*, O, N/N; *Thryothorus genibarbis*, FU, B/-; *T. coraya*, FU, N/N; *T. leucotis*, FU, N/N; *Troglodytes aedon*, O, N/N; *Henicorhina leucosticta*, FU, -/N; *Microcerculus marginatus*, FU, B/N; *M. bambla*, FU, B/B; *Cyphorhinus arada*, FU, N/N; *Donacobius atricapilla*, O, N/N.

POLIOPTILIDAE: *Microbates collaris*, FU*, B/B; *Ramphocaenus melanurus*, FU, N/N; *Polioptila plumbea*, O, N/N; *P. guianensis*, FC, N/-.

TURDIDAE: *Turdus leucomelas*, O, N/-; *T. ignobilis*, O, N/N; *T. lawrencii*, FU, N/N; *T. fumigatus*, FU, N/N; *T. hauxwelli*, FU, -/N; *T. nudigenis*, O, N/-; *T. albicollis*, FU, N/N.

MIMIDAE: *Mimus saturninus*, O, N/-.

MOTACILLIDAE: *Anthus lutescens*, O, N/-.

PARULIDAE: *Geothlypis aequinoctialis*, O, N/-; *Basileuterus rivularis*, O, N/-; *Granatellus pelzelni*, FC, N/- [incertae sedis].

COEREBIDAE: *Coereba flaveola*, O, N/-.

THRAUPIDAE: *Schistochlamys melanopis*, O, N/B; *Cisopis leverianus*, O, -/N; *Lamprospiza melanoleuca*, FC*, N/-; *Nemosia pileata*, O, N/N; *Thlypopsis sordida*, O, -/N; *Eucometis penicillata*, FU, N/N; *Tachyphonus cristatus*, FC, N/N; *T. rufiventer*, FU, -/B; *T. surinamus*, FU, N/N; *T. luctuosus*, FC, N/N; *T. rufus*, O, N/-; *T. phoeniceus*, O, N/N; *Lanio fulvus*, FC, B/B; *L. versicolor*, FC, B/B; *Ramphocelus nigrogularis*, FU, N/N; *R. carbo*, O, N/N; *Thraupis episcopus*, O, N/N; *T. palmarum*, O, N/N; *Tangara mexicana*, O, N/N; *T. chilensis*, FC, N/N; *T. schrankii*, FC, N/N; *T. xanthogastra*, FC, -/N; *T. punctata*, FC, N/N; *T. varia*, FC, N/-; *T. gyrola*, FC, -/N; *T. cayana*, O, N/-; *T. nigrocincta*, O, -/N; *T. velia*, FC, N/N; *T. callophrys*, FC, -/N; *Tersina viridis*, O, N/N; *Dacnis lineata*, FC, N/N; *D. flaviventer*, FC, N/N; *D. cayana*, O, N/N; *Cyanerpes nitidus*, FC, N/N; *C. caeruleus*, FC, N/N; *C. cyaneus*, O, N/N; *Chlorophanes spiza*, FC, N/N; *Hemithraupis guira*, O, N/N; *H. flavicollis*, FC, N/N; *Conirostrum speciosum*, O, N/N; *C. bicolor*, FC, N/-; *C. magaritae*, FC, N/N; *Piranga flava*, O, N/-; *Habia rubica*, FU, N/N.

EMBERIZIDAE: *Zonotrichia capensis*, O, N/-; *Ammodramus humeralis*, O, N/-; *A. aurifrons*, O, N/N; *Sicalis columbiana*, O, N/N; *S. luteola*, O, N/-; *Emberizoides herbicola*, O, N/-; *Volatinia jacarina*, O, N/N; *Sporophila schistacea*, O, N/-; *S. plumbea*, O, N/-; *S. americana*, O, N/N; *S. nigricollis*, O, N/N; *S. leucoptera*, O, N/-; *S. bouvreuil*, O, N/-; *S. minuta*, O, N/-; *S. castaneiventris*, O, N/N; *Oryzoborus angolensis*, O, N/N; *O. crassirostris*, O, B/B; *O. maximiliani*, O, N/-; *Arremon taciturnus*, FU, N/N; *Paroaria gularis*, O, N/N.

CARDINALIDAE: *Caryothraustes canadensis*, FC, N/-; *Parkerthraustes humeralis*, FC, -/N; *Periporphyrus erythromelas*, FU, N/-; *Saltator grossus*, FU, N/N; *S. maximus*, O, N/N; *S. coerulescens*, O, N/N; *Cyanocompsa cyanoides*, FU, N/N.

ICTERIDAE: *Psarocolius angustifrons*, O, N/N; *P. viridis*, FC, N/N; *P. decumanus*, O, N/N; *P. bifasciatus*, FC, N/N; *Clypicterus oseryi*, FC, -/N; *Ocyalus latirostris*, O, -/N; *C. solitarius*, FU, N/N; *C. cela*, O, N/N; *C. haemorrhous*, FC, N/N; *Icterus icterus*, O, N/N; *I. cayanensis*, O, N/B; *I. chrysocephalus*, O, B/B [herein treated as distinct from preceding species]; *Gymnomystax mexicanus*, O, N/N; *Lampropsar tanagrinus*, O, N/N; *Chrysomus cyanopus*, O, N/-; *C. ruficapillus*, O, N/-; *C. icterocephalus*, O, N/N; *Molothrus oryzivorus*, O, N/N; *M bonariensis*, O, N/N; *S. militaris*, O, N/N; *S. magna*, O, N/-.

FRINGILLIDAE: *Euphonia plumbea*, FC, N/-; *E. chlorotica*, O, N/N; *E. violacea*, O, N/B; *E. laniirostris*, O, N/N; *E. chrysopasta*, FC, N/N; *E. minuta*, FC, N/N; *E. xanthogaster*, FU, -/N; *E. rufiventris*, FC, B/N; *E. cayennensis*, FC, N/-.