Contribution of River-created Habitats to Bird Species Richness in Amazonia

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ABSTRACT

A substantial portion (15%) of the non-aquatic avifauna of the Amazon Basin is restricted to habitats created by rivers. These habitats are divided into six categories: beaches and sandbars, sandbar scrub, river edge forest, varzea forest, transitional forest, and water-edge. Lists of species restricted to these habitats are presented; for many of these species, this is the first published information on habitat preferences. As many as 169 bird species in the lowland neotropics may have evolved in Amazonian river-created habitats, with 99 of these spreading secondarily to man-made second-growth or to regions outside the Amazon Basin. Neither the Congo or Mississippi basin avifaunas show such a high percent of species restricted to river-created habitats; this difference is almost certainly due to the greater amplitude of seasonal water level fluctuations of the Amazon River and its tributaries and consequent greater extent of riverine habitats. Alteration of seasonal water flow patterns that would destroy these habitats could potentially exterminate 64 species of Amazonian river-created habitat specialists. The use of mist nets to sample bird community composition is discussed.

NOWHERE IN THE WORLD IS BIRD SPECIES RICHNESS greater than in the Amazon River basin, both in terms of species inhabiting the region as a whole (Amadon 1973) and coexisting at any given point (Pearson 1977). In comparison with temperate regions, year-round availability of fruit and flowers (Orians 1969, Karr 1971) and very large insects (Schoener and Janzen 1968, Schoener 1971) account for much of the high alpha-diversity in the tropics, with smaller contributions from resources such as army ants (Willis and Oniki 1978), bamboo thickets (Parker and Remsen, ms.), and special foraging substrates (Orians 1969, Terborgh 1980). The large number of Pleistocene refugia within and adjacent to the Amazon Basin (Haffer 1969, 1974; Terborgh 1980) may also contribute to the high regional diversity. The purpose of this paper is to point out the contribution of river-created habitats, developed to a much greater extent in Amazonia than anywhere in the world, to regional diversity of Amazonian birds.

Rivers throughout the world tend to produce habitats on their banks that differ in plant and animal composition from adjacent habitats. But nowhere do riverine habitats occupy such extensive areas as in the Amazon Basin. High amplitude (8–15 m) seasonal fluctuations in water levels in the river that carries one-fifth of all the planet's fresh water inundate areas from a few meters to several kilometers inland from the banks. These areas remain flooded from three to six months. The flood season is not a catastrophe but a predictable event to which the biota of the floodplain is adapted and upon which it may be dependent. See Ducke and Black (1953), Meggers (1971), Meggers *et al.* (1973), and Pires and Prance (1977) for overviews of Amazon flood ecology, hydrology, and floristics of flooded habitats.

STUDY AREAS

Localities visited with approximate duration of visits are as follows: COLOMBIA: (1) Colombian bank of the Amazon river from Leticia to Puerto Nariño, with most time spent on Isla de Santa Sofía II and nearby Quebrada Tucuchira (9 mos.); PERU: (1) Río Cayarú, a small tributary of the Amazon on the Peruvian bank in extreme northeastern Dpto. Loreto (6 days); (2) Río Javarí, the border between Peru and Brazil (7 days); (3) lower Río Napo, Dpto. Loreto (47 days); (4) Río Cenepa drainage, Dpto. Amazonas, Peru (12 days); (5) Yarinacocha area, near Pucallpa, on the Río Ucayali, Dpto. Loreto (12 days); (6) Tingo María area, upper Río Huallaga, Dpto. Huánuco (1 month); (7) Río Tambopata-Río La Torre area, Dpto. Madre de Dios (5 mos.); and (8) Cocha Cashu, Manu National Park, Dpto. Madre de Dios (2 mos.); BOLIVIA: (1) Tumichucua area, near Riberalta, Río Beni, Dpto. Beni (2 mos.); (2) Río Yata area, about 200 km south of Riberalta, Dpto. Beni (1 month); (3) upper Río Beni, about 20 km by river north of Puerto Linares, Dpto. La Paz (5 weeks); and (4) Río Isiboro-Río Chipiriri area, Dpto. Cochabamba (17 days). Thus, our field experience is limited to that portion of the Amazon Basin west of Brazil; we are uncertain to what extent this geographic bias has affected our results and interpretations.

HABITATS

Within the broad category of "river-created" habitats, we distinguish six main habitat types, the first five of which are assumed to represent sequential, successional habitat stages (see Fig. 1):

1. BEACHES AND SANDBARS. Included in this category

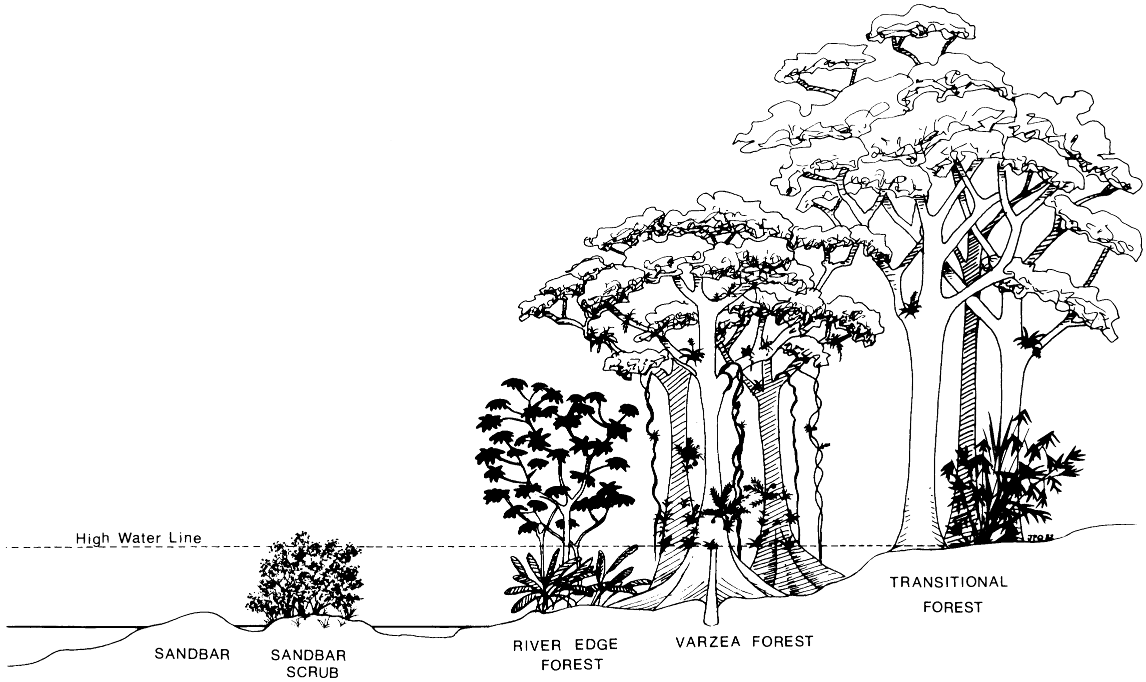

FIGURE 1. Schematic representation of five (presumably) seral stages in river-created habitats along large rivers in western Amazonia (drawing by John P. O'Neill).

are the sandy or bare mud shorelines of portions of some rivers. Sandbars are present mainly outside the flood season. They have very little or no vegetation, although often littered with tangles of vegetative debris.

2. SANDBAR SCRUB. As sandbars and some extensive beaches accumulate through time sufficient mass and height to allow them to be somewhat immune to the eroding action of the river, a low brushy growth 1–2 m in height dominated by *Tessaria integrifolia* or *Salix humboldtiana* (Ducke and Black 1953) may develop. This ephemeral vegetation is covered by water during high water season.

3. RIVER EDGE FOREST. Some sandbars become large enough and persist long enough that a forest of low stature and species diversity develops. The channels of the Amazon River and its large tributaries are a maze of such islands. This forest is dominated by such widespread tree genera as *Cecropia, Ochroma,* and *Erythrina*; *Heliconia* is perhaps the dominant genus in the understory. Cane (*Gynerium*) forms dense stands in many places. Canopy height depends on the maturity of the forest; 20–25 m might be typical. Since the eroding action of the river constantly eats away at such islands, the oldest forest is always at the upstream end, with a gradient in decreasing age towards the downstream end, where silt is usually being deposited, making up for losses at the upstream end. Thus these islands are in a sense continually moving downstream. River edge forest is found not only on such islands but also on banks of large rivers wherever forces of the river current are strong enough to keep the forest in an early stage of succession.

4. VARZEA FOREST. In areas seasonally or permanently inundated where the force of the river current is weak, a forest develops that is much taller and more diverse than the river edge forest. Except for the extensive edge effect along rivers and lakes, this forest seems to resemble "terra firme" (never-flooded) forest in structure more than river edge forest; canopy height in mature "varzea" forest is close to 30 m, buttressed trees are common (virtually absent in river edge forest), and a few "canopy emergents" are present. We have never seen this forest type on river islands, although it may be present on some very large islands. High-water marks on trunks are usually 1–2 m from the ground.

The extent and location relative to the river bank of varzea forest depends greatly on height of the river bank; the higher the bank, the farther back from the shoreline will varzea forest be found and the greater the extent of the river edge forest between the low-water season shoreline and the varzea forest. Thus as one travels up a tributary, the band of varzea forest on the banks gradually becomes narrower, eventually disappearing altogether, leaving a band of river edge forest that also gradually narrows (see Diamond and Terborgh 1967). Varzea forest in the lower Amazon River in Brazil is flooded twice daily by tides.

5. TRANSITIONAL FOREST. This is low-lying, poorly-drained forest seasonally inundated by rainfall or by rain-swollen streams, but not by a nearby river. Structurally it is similar to terra firme. Palms are common in the swampy places and bamboo (especially *Guadua*) is also conspicuous. This forest type differs from varzea in having a more developed undergrowth.

6. WATER-EDGE HABITATS. In this category we include a variety of habitats immediately adjacent to shorelines: emergent aquatic vegetation, marsh grasses (especially *Paspalum*) and "floating meadows" (Junk 1970, 1973) that line oxbow lakes and sections of some streams, and bushes and small trees growing adjacent to or over slow-moving water.

METHODS

Habitat preferences were recorded on a daily basis for all bird species observed in river-created habitats as well as in upland (terra firme) habitats. Voucher specimens were collected for species difficult to identify by sight. Specimens were deposited at the Museum of Zoology, Louisiana State University, and the Museum of Vertebrate Zoology, University of California, Berkeley.

For analysis of the importance of river-created habitats to overall Amazonian bird species richness, each species breeding within forested lowland Amazonia was placed in one of six habitat-range categories: (A) found only in river-created habitats and not occurring outside the forested lowlands of the Amazon-Orinoco basins, except perhaps in the Guianan lowlands; (B) same range as Category A, but also found outside river-created habitats in second-growth forest, scrub, and pastures; (C) same habitats as Category A, but geographic range extends beyond the Amazon-Orinoco-Guiana lowlands, some species as far north as eastern Panama or as far south as Misiones, Argentina; true savanna or campo species are excluded; (D) same habitats as in Category B and same range as in Category C; (E) found only in river-created habitats within Amazonia, but range extends north of eastern Panama or south of Misiones; (F) any other combination of habitat (*e.g.*, terra firme) and range not covered by Categories A–E.

The sequence of Categories A–E roughly corresponds to a gradient of decreasing degree of likelihood that member species evolved in river-created habitats in the Amazon Basin. Appropriate terms reflecting the unavoidable subjectivity in determining this sequence might be "almost certainly" for Category A, "probably" for B and C, and "maybe" for D and E. The rationale for ranking species in habitat-range Category B so high is that only with the relatively recent arrival of man in the Amazon has second-growth habitat been available (Terborgh and Weske 1969) except for small patches around large tree-falls; thus we believe that for most of their evolutionary history, these species must have been restricted to river-created habitats. Terborgh and Weske (1969) argued that all second-growth bird species in extreme western Amazonia are derived from either terra firme or river-created habitats.

A conservative bias in our assessment of the evolutionary contribution of river-created habitats is that Category F contains many species that may have evolved in river-created habitats. For example, there are approximately 140 species restricted to the Amazon-Orinoco-Guianas region that occur in both river-created habitats and terra firme forest (*e.g.*, *Pionites* spp., *Otus watsonii*, *Pteroglossus inscriptus*, *Euphonia rifuventris*). Some species with this type of distribution could have first evolved in river-created habitats and then spread secondarily to upland forest. One could also speculate that at least some species found as far north as Middle America or as far south as central Argentina in river-created habitats, second-growth, and savanna (all relegated here to category F) could have first originated in river-created habitat; we list these species in Appendix II. Also included in Category F are 25 species for which we could find no habitat information; several of these may be restricted to river-created habitats (*e.g.*, *Picumnus varzeae*). Species that take their food directly from water, *e.g.*, kingfishers, most "waterbirds," and some raptors, were excluded from the analysis.

RESULTS AND DISCUSSION

IMPORTANCE OF AMAZON RIVER-CREATED HABITATS.—Numbers of species in the various habitat and range categories for the Amazon drainage are presented in Table 1. In Appendix I we present lists of species for each of the habitat-range categories. The species restricted to river-created habitats (Categories A, C, and E) comprise 15.0 percent of the total land bird avifauna of the Amazon Basin. If waterbirds had also been included, the percentage would have been higher.

How does this contribution to regional diversity by river-created habitats in the Amazon compare to other major river systems in other regions? For comparison to another tropical river system, we examined habitat preferences of birds of the Congo drainage of Africa with Chapin (1932, 1939, 1953, 1954) and A. Brosset (in litt.) as our sources for habitat information. It appears that only 12 species (5.6% of the total landbird avifauna, Appendix III) are restricted to river-created habitats and occur entirely within the forested lowlands of West Africa (*i.e.*, equivalent to Category A species in Amazon). This is a significantly smaller (Chi-Square, $P < 0.05$) contri-

TABLE 1. *Numbers of non-aquatic bird species in six habitat-range categories (see Methods for definitions) for the avifauna of the forested lowlands of the Amazon drainage.*

Habitat-Range category	S (percent total avifauna)
A	70 (10.3%)
B	29 (4.3%)
C	20 (2.9%)
D	38 (5.6%)
E	12 (1.8%)
A–E combined	169 (24.9%)
F	511 (75.1%)
Total	680

bution to the total avifauna than in the Amazon, and in absolute number of species, there are six times as many Category A species in the Amazon than in the Congo. Because of our unfamiliarity with the avifauna of Africa, we did not attempt comparisons beyond Category A species.

For comparison to a major drainage system at temperate latitudes, we examined habitat preferences of birds of the Mississippi River drainage of the forested lowlands of eastern North America considering the Atlantic coastal lowlands as equivalent to the Orinoco-Guyana lowlands. From published information on habitat preference and from our own experience, we considered only five species to be equivalent to Category A or B Amazon species: *Campephilus principalis, Protonotaria citrea, Limnothlypis swainsoni, Vermivora bachmani,* and *Wilsonia citrina.* This is only 2.1 percent of the landbird avifauna of the region (excluding species restricted to grasslands, the southeastern pine forests, or the Appalachian Mountains). This is significantly lower in proportion (Chi-Square, $P < 0.01$) and in absolute number of Category A and B species than in the Amazon. Furthermore, each of the five North American species has been reported breeding in upland habitats in some portion of its range.

What explains the much greater absolute and relative number of species restricted to river-created habitats in the Amazon? We propose that this is related in part to the much greater areal extent of these habitats in Amazonia (due to greater amplitude of seasonal water level fluctuations) than in any other region in the world. The larger the area involved, the lower the probability that long-term climatic changes will reduce it in size to the point at which species will begin to go extinct. Unfortunately, quantitative measures of the extent of these habitats in the three river basins were not available.

ECOLOGY AND ZOOGEOGRAPHY OF RIVER-CREATED HABITAT BIRDS.—The bird species composition of Amazonian river-created habitats is generally distinct from that of adjacent terra firme forest. As expected from radical differences in habitat structure, beaches and sandbars and sandbar scrub share no species with the terra firme forest except for a few aerial foragers (vultures, swifts). As for river edge forest, of 93 regularly occurring landbird species on Remsen's Isla de Santa Sofí II site in the Amazon River, only seven (7.5%) are found in terra firme forest: *Cathartes aura, Pionus menstruus, Amazona farinosa, Chaetura cinereiventris, Cotinga maynana, Psarocolius decumanus,* and *Cacicus cela.* Comparable figures for varzea forest are not available, but our qualitative assessment is that a much higher percentage of species found in varzea are also found in terra firme. Transitional forest, the most advanced of the successional stages and most similar to terra firme forest, shows a fairly high degree of species-sharing. Of 233 residents of transitional forest at Parker's Río Tambopata site, 156 (67.0%) were also found in nearby terra firme forest.

In Dpto. Ayacucho, Peru, Terborgh and Weske (1969) found that only 28 (28.2%) of 99 riverine habitat species, primarily river edge forest species, were found in adjacent nonriverine forest. Even this degree of sharing is conservatively biased, because the terra firme forest at their upper Apurímac Valley site is notably depauperate (Terborgh and Weske 1969), resulting in apparent ecological release in the form of a habitat shift by several species. For example, in the absence of *Monasa morphoeus* and *Piaya melanogaster,* their congeneric replacements in river-created habitats, *M. nigrifrons* and *P. cayana* are found in terra firme forest. We have observed similar habitat expansion of species typical of river-created habitats into relatively depauperate terra firme forest in the foothills of the eastern Andes in Peru and Bolivia by *Pipile pipile, Trogon curucui, T. collaris, Pteroglossus castanotis, Myrmeciza melanoceps, M. goeldii, Hylopezus berlepschi, Cephalopterus ornatus, Neopelma sulphureiventer, Thryothorus genibarbis, Cissopis leveriana, Ramphocelus carbo,* and *Psarocolius angustifrons.*

The reasons for the distinctness of the avifauna of river-created habitats are probably both ecological and historical. The relative contributions of these two factors is extremely difficult to measure (Endler 1982). One ecological factor is the enormous difference in habitat structure between terra firme forest and all river-created habitats except varzea forest and transitional forest that make it unlikely that they would share any species except extreme habitat generalists. Flooding and its reduction of forest undergrowth is presumably responsible for a scarcity of understory species that occur in both varzea and terra firme forest.

In a historical context, forest almost certainly persisted along major river courses in Amazonia at the height of the dry interglacial periods in the Pleistocene, even when the extent of terra firme forest was drastically reduced

(Haffer 1974). The hypothetical Pleistocene forest refugia mapped by Haffer for birds (1974: 151) are mainly away from the courses of the Amazon and its major tributaries. Thus river-created habitats, at least those (varzea forest, beaches and sandbars, and sandbar scrub) most highly restricted to large rivers, may have been geographically isolated from terra firme forest, setting up conditions conducive to differentiation. Higher sea levels, however, may have placed riverbank habitats adjacent to terra firme refugia.

Closely related species pairs (such as *Monasa nigrifrons* and *M. morphoeus, Piaya cayana* and *P. melanogaster, Myrmoborus lugubris* and *M. myotherinus,* and *Schiffornis major* and *S. turdinus*) that usually replace each other abruptly at the riverine habitat-terra firme boundary provide some support for the importance of historical factors. Also, river-created habitat specialists include a disproportionately high number of monotypic genera (and one monotypic family, Opisthocomidae) compared to terra firme forest: out of 102 species in Categories A, C, and E, 16 (15.7%) belong to monotypic genera, whereas of the 265 species restricted to terra firme forest, only 20 (7.6%) belong to monotypic genera (Chi-Square = 5.6, $P < 0.02$). Classical zoogeography would interpret this as evidence for the antiquity and isolation of river-created habitats from terra firme forest, although strong selection pressure due to ecological differences could hypothetically produce the same degree of differentiation (Endler 1973).

The influence of the Amazon River on bird habitats may extend beyond the boundaries of today's inundation zone. The series of ridges formed by the ancient river bed and roughly paralleling the current river course may create habitats recognized by birds as distinct from adjacent forest that has *never* been flooded. It would be enlightening to survey vegetation along the ancient river banks to see if and how it differs floristically and structurally from surrounding forest and to see if there are bird species restricted to one or the other.

Because of the ephemeral nature of most river-created habitats, birds specializing on these successional habitat stages are probably very good dispersers compared to terra firme forest birds. No data yet exist with which to test this hypothesis directly, much less to distinguish greater dispersal ability from greater historical continuity of habitat, but a corollary of the hypothesis can be examined. With increased potential gene flow among populations, there should be less geographic variation in river-created habitat species than terra firme forest species. In Table 2, we compare the degree of taxonomically recognized geographic differentiation in species from Category A to randomly drawn terra firme forest species restricted to the Amazon-Orinoco-Guiana lowlands. The difference in tendency to show geographic variation is significantly lower in river-created habitat birds (Chi-Square, $P < 0.001$).

TABLE 2. *Geographic differentiation in river-created habitat birds vs. terra firme forest birds. River-created habitat species from Category A are compared to a sample of terra firme forest birds randomly selected from species found only in terra firme forest and restricted to the Amazon-Orinoco-Guiana lowlands. To control for possible familial level differences in tendency to form subspecies, the selection of terra firme birds was done on a family-by-family basis, taking the number of species equivalent to the number of species in that family in Category A. The smaller sample of terra firme forest species reflects our inability to find an equivalent number of appropriate species within a family in many cases.*

	Number of species	
	River-created habitats	Terra firme forest
Monotypic forms	47	12
Polytypic forms[a]	20	36

[a] A species was considered polytypic if subspecies have been described or if the selected species was a member of a superspecies group within the Amazon Basin. Thus the total number of river-created habitat forms examined is reduced by three because six species in Category A are allospecies of one another (*Galbalcyrhynchus leucotis* and *G. purusianus, Myrmeciza melanoceps* and *M. goeldii,* and *Hypocnemoides maculicauda* and *H. melanopogon*).

Some anecdotes and circumstantial evidence help to illustrate the relatively greater dispersal ability needed as an adaptation for inhabiting river-created habitats. Tropical tinamous (Tinamidae) would usually be considered very poor dispersers by most naturalists and among the least likely birds to cross open water. Yet near Leticia, Colombia in June 1975, during the transition from high-water to low-water season, Remsen saw a *Crypturellus undulatus,* a common bird in river edge forest, fly approximately 500 m across open water of the Amazon River from the mainland to a small, forested island. This species is absent from such islands during high-water season, when they are almost completely flooded, but is common the rest of the year. Thus they must regularly cross expanses of open water to colonize these islands on a seasonal basis.

Antbirds (Formicariidae) are another family generally considered to be highly sedentary and unlikely to be good dispersers. Yet three of the most characteristic species of islands in the Amazon River, *Myrmoborus lugubris, Myrmochanes hemileucus,* and *Thamnophilus cryptoleucos,* must cross up to two km of open water to colonize such islands, most of which are never connected to the mainland.

In light of their presumed excellent dispersal abilities, it may be asked how the geographic range of any river habitat species could be sufficiently fragmented to interrupt gene flow and promote allopatric speciation or even subspecific differentiation (J. Terborgh, pers. comm.). It is difficult to envision past climates in Amazonia so severely arid that riverine habitat was not continuous, and so the mechanics of the speciation process in these birds is of great interest. The subspecific differentiation in presumably perpetually contiguous populations or riverine habitat species provides weak evidence for the importance of natural selection rather than absence of gene flow in the differentiation process (Endler 1973).

The distinctive nature and often large width (up to one km in upper Amazon, much wider in lower Amazon) of the band of river-created habitat on the banks of major tropical rivers increase their effectiveness as barriers to dispersal of terra firme forest species. Rivers form the boundaries between several allospecies and numerous subspecies in Amazonia (Haffer 1969, 1974; Willis 1969), a situation found only rarely elsewhere in the world. For example, we cannot find a single case of different allospecies or subspecies occurring on opposite banks of the same river in North America or Middle America.

DETERMINING HABITAT PREFERENCES.—A source of frustration in our analysis is the primitive state of knowledge concerning habitat preferences of Amazon birds. For instance, there are probably differences in species composition between "white-water" and "black water" river-created habitats and between permanently flooded swamp forest ("igapó") and seasonally flooded varzea forest.

Oxbow lakes may have species found only at their margins. We have tried to be as conservative as possible in placing species in Category A, but as more information is accumulated, membership in our various categories will certainly have to be modified. Virtually everyone (see Acknowledgments) who commented on our habitat list noted one or more of the species that we consider river-created habitat specialists in some non-riverine habitat on some occasion. Although we feel that many of these observations were of wandering birds rather than residents, we are surprised by the degree of geographic and local variation in habitat preference of some Amazon species. Since man-created second-growth is a relatively new habitat in Amazonia, regional differences in degree of occupancy of such habitats by riverine birds is expected; it is unlikely that the extent of adaptation to these new habitats is at an equilibrium state.

Although more detailed studies of habitat preferences of Amazon birds are obviously needed, we caution against the increasing tendency of field ornithologists to rely on mist net captures for determining habitat preferences and relative abundances (*e.g.*, Lovejoy 1974, Wilson and Moriarity 1976, Karr 1980, Kikkawa *et al.* 1980). We have spent a combined total of 39 months in field camps in tropical latitude forests in which relative abundances of bird species were monitored both by mist net capture rates and by visual and auditory censuses. In our experience, mist nets seem to catch a disproportionate number of non-breeding, non-resident individuals presumably dispersing through the habitat rather than territorial local residents that should be the targets for community analyses. We believe that individual birds that would be clearly distinguishable to a temperate zone ornithologist as local dispersers and migrants (due to a more synchronized and compressed community breeding season) are not recognized as such by the tropical zone ornithologist, who, without intensive local banding, territory marking, and censuses of singing birds, cannot distinguish residents from dispersers. Tropical birds, with their longer breeding seasons, produce dispersing individuals throughout much of the year; and these dispersers, with their lower degree of site-familiarity and higher mobility, are much more likely than residents to be captured by mist nets.

As for measuring relative abundance, we again feel that too much faith has been put on mist net capture rates. We believe that (1) average distance travelled between foraging sites, and (2) social system, contribute as heavily to frequency of capture as does true relative abundance. Thus, species that move relatively long distances between feeding sites and those that do not have "type A" territories should be disproportionately represented in mist net samples. Indeed, genera that fit these criteria, such as *Pipra, Manacus, Chiroxiphia, Pipromorpha, Mionectes, Glyphorhynchus, Phaethornis,* and *Threnetes,* are usually listed as the most "abundant" species in tropical community samples (Karr 1971, Lovejoy 1974). Although we certainly agree that these birds are often among the most common species in tropical forests, our daily census data and our intuitive impressions from extensive field experience lead us to believe that published data on relative abundance of these birds are drastic overestimates (*e.g.*, two most common small frugivores, *Pipra erythrocephala* and *Manacus manacus,* 30 times more abundant than the two most common small insectivores reported by Snow and Snow [1971]). Fortunately, most authors who rely primarily on mist net samples for analyzing community structure are well aware of some of the biases in mist net data (*e.g.*, Karr 1971, 1981; Lovejoy 1974).

The differences between studies relying primarily on mist net capture data and one (Pearson 1975) that relied primarily on vocal-visual census data are striking: Pearson does not list a single species from the genera listed above among his "common" species (42 species) from three Amazonian forest sites. Pearson's censuses probably underestimate these net-prone genera, but we suspect that Pearson's data more closely represent true relative abundance than those produced by mist nets. We do not feel that species of net-prone genera are any more difficult to detect visually or vocally than are other forest birds. Whatever those characteristically quiet species (female manakins, *Mionectes, Pipromorpha*) lose in detectability by being silent is more than compensated for by their lack of fear of observers; these species in our experience are among the tamest of forest birds. We feel that accurate relative abundances can only be estimated in a quasi-quantitative way through visual-auditory censuses by very experienced observers combined with some mist-netting (*e.g.*, Terborgh and Weske 1969, Terborgh 1971).

CONSERVATION.—The contribution of river-created habitats to overall Amazonian bird species richness and the high number of species restricted to river-created habitats in the Amazon Basin has important implications for conservation in Amazonia. Presumably other animal and plant groups show a comparable pattern of habitat restriction, although data do not seem to be available. Any alteration of water flow patterns in the Amazon, such as by an increased amplitude of flood crest due to deforestation (Gentry and Lopez-Parodi 1980) or by damming the river course itself, would almost certainly have deleterious effects on river-created habitats, especially those dependent on seasonal inundation. If a dam prevented or reduced seasonal water level fluctuations, the extent and diversity of river-created habitats would certainly also be reduced, perhaps to the point at which only some water-edge character (*e.g., Galbalcyrhynchus* spp.), leaving most replaced riverine habitats. In the extreme, the only river-dependent bird species that would not disappear would be those restricted to such habitats only because of their species in Category A vulnerable to extinction, and an additional 25 species from Categories C and E subject to extirpation from the Amazon; thus, overall Amazon bird species richness could potentially be reduced by approximately 13 percent if the natural pattern of water level fluctuation was altered throughout Amazonia.

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Appendix I.—Species of the habitat-range categories used in Table 1. Numbers in parentheses refer to habitat preferences: 1. Beaches and Sandbars, 2. Sandbar Scrub, 3. River Edge Forest, 4. Varzea Forest, 5. Transitional Forest, 6. Water-edge Habitats (see Habitats section for habitat descriptions), and 7. Man-made second-growth.

Category A. Species restricted to river-created habitats and found only in forested Amazon-Orinoco-Guiana lowlands:

Leucopternis schistacea (4, 5)
Crax globulosa (3, 4)
Anhima cornuta (1, 6)
Brotogeris sanctithomae (3, 4)
Graydidasculus brachyurus (3)
Amazona festiva (3, 4)
Opisthocomus hoazin (6)
Chordeiles rupestris (1)
Hydropsalis climacocerca (1, 2, 6)
Phaethornis hispidus (3, 4, 5)
Leucippus chlorocercus (2)
Galbalcyrhynchus leucotis (3, 6)
Galbalcyrhynchus purusianus (3, 6)
Brachygalba albogularis (3)
Bucco tamatia (4)
Capito aurovirens (3, 4, 5)
Picumnus rufiventris (3, 5)
Celeus spectabilis (3, 5)
Nasica longirostris (3, 4)
Furnarius minor (2)
Furnarius figulus (R. S. Ridgely, pers. comm.)
Synallaxis propinqua (2)
Cranioleuca gutturata (3, 5, 6)
Certhiaxis mustelina (6)
Automolus melanopezus (5)
Automolus rufipileatus (3, 5)
Simoxenops ucayalae (3, 5)
Berlepschia rikeri (6, in palms)
Sakesphorus luctuosus (R. S. Ridgely, pers. comm.)
Thamnophilus cryptoleucus (3)
Myrmotherula assimilis (3)
Drymophila devillei (5)
Myrmoborus lugubris (3)
Myrmoborus melanurus (3, 5)
Sclateria naevia (4, 5, 6)
Hypocnemoides melanopogon (4, 5, 6)
Hypocnemoides maculicauda (4, 5, 6)
Myrmochanes hemileucus (2)
Percnostola lophotes (3, 5)
Myrmeciza hyperythra (4, 5)
Myrmeciza goeldii (5)
Myrmeciza melanoceps (5)
Cephalopterus ornatus (3, 4)
Todirostrum maculatum (2, 3, 6)
Poecilotriccus tricolor (5)
Hemitriccus johannis (3)
Hemitriccus flammulatus (5)
Stigmatura napensis (2)
Serpophaga hypoleuca (2)
Gymnoderus foetidus (3, 4, 5)
Schiffornis major (3, 4)
Muscisaxicola fluviatilis (1)
Knipolegus orenocensis (2, 6)
Knipolegus poecilocercus (6)
Ochthoeca littoralis (1)
Attila bolivianus (3, 4, 5)
Attila cinnamomus (3, 4)
Attila citrineiventris (4)
Ramphotrigon fuscicauda (5)
Elaenia pelzelni (2, 3)
Myiopagis flavivertex (4, 5)
Atticora fasciata (1)
Oryzoborus crassirostris (6)
Paroaria gularis (1, 2, 6)
Ramphocelus nigrogularis (3, 4, 6)
Conirostrum margaritae (3)
Ocyalus latirostris (4)
Psarocolius viridis (4)
Lampropsar tanagrinus (4)
Agelaius xanthophthalmus (6)

Category B. Species found in river-created habitats and also second-growth, edge situations, or savannas away from riparian habitat, and found primarily within the forested Amazon-Orinoco-Guiana lowlands:

Daptrius ater (1, 3, 6, 7)
Aratinga weddellii (3, 4, 7)
Threnetes leucurus (3, 5, 7)
Phaethornis stuarti (5, 7)
Campylopterus largipennis (3, 5, 7)
Amazilia fimbriata (3, 7)
Bucco macrodactylus (3, 7)
Monasa flavirostris (3, 5, 7)
Chelidoptera tenebrosa (3, 7)
Eubucco tucinkae (3, 6)
Pteroglossus inscriptus (4, 5, 7)
Picumnus castelnau (3, 7)
Melanerpes cruentatus (3, 4, 5, 7)
Melanerpes rubrifrons (?3, ?4, 7)
Synallaxis albigularis (2, 7)
Thamnophilus amazonicus (3, 7)
Cercomacra nigrescens (3, 7)
Hypocnemis cantator (3, 5, 7)
Myrmeciza atrothorax (2, 3, 6, 7)
Hylopezus berlepschi (3, 7)
Neopelma sulphureiventer (3, 7)
Todirostrum chrysocrotaphum (4, 5, 7)
Thryothorus guarayanus (3, 6, 7)
Turdus ignobilis (3, 7)
Cyanocorax violaceus (3, 7)
Sporophila castaneiventris (6, 7)
Dacnis flaviventer (3, 4, 7)
Icterus chrysocephalus (3, 6, 7)

Category C. Species restricted to river-created habitats in Amazonia but range extends beyond Amazon-Orinoco-Guiana lowlands (perhaps as far north as eastern Panama or as far south as Misiones, Argentina):

Crypturellus cinereus (5)
Crypturellus undulatus (3)
Helicolestes hamatus (6)
Buteogallus urubitinga (1, 3, 6)
Aburria pipile (3, 5)
Ara severa (3, 4)
Celeus flavus (3, 4, 5)
Furnarius leucopus (3)
Myrmotherula surinamensis (6)
Pipra fasciicauda (5)
Tyrannopsis sulphurea (6, in palms)
Pitangus lictor (6)
Cnemotriccus fuscatus (2, 3)
Hemitriccus striaticollis (2, 3)
Inezia inornata (2)
Progne tapera (1)
Donacobius atricapillus (6)
Oryzoborus maximiliani (6)
Conirostrum bicolor (3)
Agelaius icterocephalus (6)

Category D. Species found in river-created habitats, and also second-growth, edge situations, or savannas away from riparian habitats, but range extends beyond forested Amazon-Orinoco-Guiana lowlands (perhaps as far north as eastern Panama or as far south as Misiones, Argentina):

Cathartes burrovianus (1, 2, 6, 7)
Milvago chimachima (1, 2, 3, 7)
Ortalis guttata (3, 7)
Leptotila rufaxilla (3, 4, 7)
Ara manilata (4, 6, in palms)
Forpus xanthopterygius (6, 7)
Amazona amazonica (3, 4)
Piaya minuta (6, 7)
Tachornis squamata (3, 6, 7, in palms)
Glaucis hirsuta (3, 6, 7)
Anthracothorax nigricollis (3, 7)
Amazilia lactea (3, 7)
Chlorestes notatus (3, 6, 7)
Hylocharis cyanus (3, 5, 7)
Trogon curucui (3, 5, 7)
Nonnula ruficapilla (3, 5, 7)
Monasa nigrifrons (3, 4, 5, 7)
Pteroglossus castanotis (3, 4, 7)
Colaptes punctigula (3, 7)
Campephilus melanoleucos (3, 4, 7)
Xiphorhynchus picus (3, 7)
Myiozetetes cayanensis (6, 7)
Tyrannus albogularis (3, 6, 7)
Todirostrum latirostre (3, 7)
Elaenia spectabilis (2, 3, 7)
Tyrannulus elatus (2, 3, 7)
Phaeomyias murina (2, 7)
Campylorhynchus turdinus (3, 6, 7)
Thryothorus genibarbis (3, 6, 7)
Thryothorus leucotis (3, 4, 6, 7)
Myospiza aurifrons (2, 7)
Cissopis leveriana (2, 6, 7)
Nemosia pileata (2, 3, 7)
Ramphocelus carbo (2, 3, 6, 7)
Conirostrum speciosum (3, 7)
Psarocolius angustifrons (3, 4, 7)
Gymnomystax mexicanus (6, 7)
Icterus icterus (3, 6, 7)

Category E. Species restricted to river-created habitats but range extends beyond forested Amazona-Orinoco-Guiana lowlands north of eastern Panama or south of Misiones, Argentina:

Leptodon cayanensis (4, 5)
Aramides cajanea (3, 4)
Crotophaga major (3, 4, 6)
Synallaxis albescens (2, 6)
Cranioleuca vulpina (2)
Certhiaxis cinnamomea (6)
Fluvicola pica (1, 6)
Fluvicola leucocephala (6)
Myiophobus fasciatus (2, 6)
Tachycineta albiventer (1, 6)
Stelgidopteryx ruficollis (1)
Thlypopsis sordida (2, 3)

Appendix II.—Species placed in Category F (non-riverine) in Table 1, but which may have evolved in Amazonian river-created habitats. These species are found in river-created habitats, and also second-growth, edge situations, or savannas away from riparian habitat, but their range extends north of eastern Panama or south of Misiones, Argentina. The habitat code used in Appendix I is used here also:

Ictinia plumbea (3, 4, 7)
Elanoides forficatus (3, 4, 7)
Geranospiza caerulescens (3, 4, 5, 7)
Herpetotheres cachinnans (3, 4, 5, 7)
Columba cayennensis (3, 6, 7)
Columba speciosa (3, 7)
Claravis pretiosa (3, 7)
Pionus menstruus (3, 4, 7)
Crotophaga ani (2, 6, 7)
Glaucidium brasilianum (2, 3, 7)
Pachyramphus polychopterus (2, 3, 7)
Myiozetetes similis (2, 3, 6, 7)
Myiozetetes granadensis (2, 3, 4, 6, 7)
Pitangus sulphuratus (1, 2, 3, 4, 6, 7)
Megarhynchus pitangua (2, 3, 4, 6, 7)
Myiarchus ferox (2, 3, 7)
Elaenia flavogaster (2, 3, 7)
Camptostoma obsoletum (2, 7)
Saltator coerulescens (3, 6, 7)
Thraupis palmarum (3, 6, 7, mainly in palms)
Euphonia chlorotica (3, 7)
Euphonia laniirostris (3, 7)
Scaphidura oryzivora (1, 2, 7)
Icterus cayanensis (3, 5, 6, 7)

Appendix III.—Species restricted to river-created habitats and to the forested lowlands of the Congo River Basin (i.e., equivalent to habitat-range Category A of the Amazon River Basin).

Merops breweri
Merops malimbicus
Pseudochelidon eurystomina
Riparia congica
Hirundo nigrita
Apalis goslingi
Fraseria cinerascens
Muscicapa cassini
Anthreptes aurantium
Nectarinia congensis
Euplectes anomalus
Ploceus aurantius