

Distribution of Amazon Forest Birds

by

JURGEN HAFFER, Essen

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1. Introduction

Amazonia comprises an area of some six million square kilometers of fairly featureless tropical lowlands covered with rain forests that harbor the most species-rich flora and fauna on earth. The lack of orographic, vegetational and climatic barriers posed a challenge to biologists attempting to explain the origin of the large diversity of life in this region, as it was known since Charles Darwin and Moritz Wagner that spatial isolation of animal populations is the prerequisite of the geographic speciation process (Mayr 1942, 1963). Three theories have been proposed to solve this apparent paradox (see Haffer 1974, 1978, Simpson and Haffer 1978 for more detailed reviews)¹⁾:

1. *Tertiary island theory*: Paleogeographic changes in the distribution of land and sea in South America during the Tertiary period led to the isolation and differentiation of animal populations on islands and peninsulas of varying extent. Present species and subspecies as well as their distribution patterns are thought to have originated during the Tertiary and no faunal differentiation occurred in the tropical lowlands during the following Quaternary period.

2. *Quaternary river theory*: The development of the river system in Amazonia during the early Quaternary caused the isolation and differentiation of previously continuous and uniform populations on opposite river banks.

3. *Quaternary refuge theory*: The presently continuous neotropical forests repeatedly broke into blocks of remnant forests separated by non-forest vegetation and coalesced again under the changing climate of the Quaternary and earlier geological periods. Populations of plant and animal species isolated in the restricted forest 'refugia' during dry phases a) became extinct, b) survived without much change or c) differentiated reaching in many cases subspecies or species status before they came into secondary contact with previously conspecific populations of other forest refugia during a following period of forest expansion. Rivers probably were not a causal factor of speciation in Amazonia (except perhaps in a few cases) but merely limited or modified the dispersal of populations from the forest refugia. This theory proposes that the intensive earlier processes of faunal differentiation during the Tertiary continued into the Quaternary, as the degree of geographical isolation and the rate of differentiation of the Pleistocene refuge populations probably caused an appreciable deviation from the widespread ancestral populations.

¹⁾ These three theories concern the origin of species diversity in Amazonia as opposed to those theories which attempt an explanation of the maintenance of species diversity. The latter theories refer to the great age of stable tropical forest habitat, lack of Pleistocene extinctions, increased specialization, niche overlap, and competition in tropical forests.

In order to provide additional background data needed for an assessment of the above theories on the origin of the present faunal diversity and distributional patterns of species and subspecies in Amazonia, I discuss in this article the distribution of a large sample of Amazon forest and forest edge birds providing the first quantitative contour maps on avian distribution in tropical lowland South America. In particular, I illustrate the location and varying significance of 'distribution centers' of species and subspecies in Amazonia and demonstrate the regionally changing barrier effect of Amazonian rivers. I exclude from this analysis water birds, as their ecological correlations and distributional histories differ considerably from those of land birds. Reichholf (1975) discussed the relevant issues for South America and compared geographical trends in the fish-eating herons and 'detritus'-eating ducks. Neotropical species of herons (Ardeidae) are fairly old adaptational types and increase in number of species and individuals toward the lower latitudes in accordance with the general pattern. By contrast, ducks (Anatidae) decrease in abundance and number of species toward the tropics probably because they are in food competition with the rich tropical fish fauna. Slud (1976) also pointed out that the ratio of water bird species to land bird species drastically decreases with decreasing latitude being lowest in the humid tropics. The latter author discussed geographical patterns of the neotropical avifauna also from another viewpoint. He analysed relative proportions of the major taxonomic components of the avifauna (passerines, non-passerines, suboscines, oscines) which correlate with climate and vegetation. The suboscine proportion is highest in the Amazon forests; the non-passerine proportion decreases with increasing elevation and rainfall.

According to the conventional view, suboscines are a primitive group of passeriform birds which retreated into (or survived in) the tropical lowland forest when oscines entered South America and supposedly outcompeted the suboscines after the closure of the Panamanian land bridge during Pliocene time (Amadon 1973). An alternative theory (Willis 1977) suggests that forest edge suboscines or their direct ancestors were present in Gondwanaland and were separated by continental drift. Forest-dwelling furnarioid suboscines evolved in the New World after Africa and South America drifted apart and open-country oscines were either separated by the drift or entered South America early in the Cenozoic (see also discussions by Feduccia 1977).

Amazonia is the most extensive forest region on earth comprising continuous lowlands from the Andes mountains to the Atlantic coast (Fig. 1). As here understood, 'Amazonia' includes not only the basin of the Solimões-Amazon River and its tributaries but also the forests of southern Venezuela and of the Guianas extending northward along the Atlantic

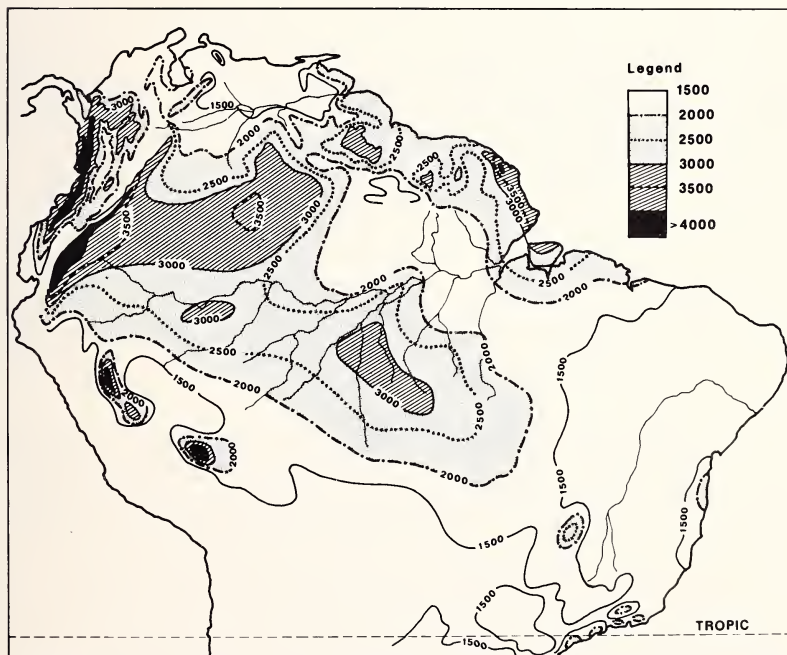


Fig. 1: Above — Distribution of humid tropical lowland forest in central and northern South America. Forests surrounding savanna regions are mostly semi-deciduous. Black areas represent Andes mountains above 1000 meters elevation (after Hafer 1969). Below — Total annual rainfall (in millimeters) in central and northern South America. After Simpson and Hafer (1978).

coast beyond the mouth of the Río Orinoco. These forests are continuous with those of the Amazon valley.

The forests of Amazonia are bordered to the north by extensive grass savannas (llanos) in eastern Colombia and central Venezuela and to the south by various other types of nonforest vegetation (cerrado and caatinga) of central and northeastern Brazil. Comparatively small open enclaves of restricted savannas and campos cerrados interrupt the forests of the upper Rio Madeira — Tapajós region and those to the north of the lower Amazon and in the upper Rio Branco Valley. Sioli (1969) and Meggers (1971), among other authors, prepared recent summaries of environmental conditions in the forested lowlands of tropical South America. Annual rainfall may be used as an ecological indicator. Regional distribution of annual precipitation is uneven and several rainfall centers exist in western, northern and eastern Amazonia (Fig. 1). The surface relief in conjunction with the annual shifting of climatic zones causes these regional inequalities of annual rainfall (Reinke 1962, several authors in Schwerdtfeger 1976).

2. Methods

I analysed the geographical ranges of about 400 bird species inhabiting forests and forest edges in Amazonia. I felt that the available locality records of these species permitted a reasonably accurate definition of their ranges. Admittedly, some of the avian ranges which I dismissed as "inadequately known" (because only widely scattered records from portions of Amazonia are available) may prove to be representative for species of extremely patchy occurrence. Subspecies of some species have been taken into consideration if they are geographically isolated or, in cases of continuous distribution, if the population structure of the species concerned (i. e. the nature of the subspecies) was known to the author¹⁾. Extensive collections of birds from most parts of Amazonia have become available during the past one hundred years and led to the publication of several regional catalogues and numerous faunistic reports²⁾. However, a summarizing distributional analysis has not been attempted for this region. Over the past several years,

¹⁾ In biogeographical studies, the unqualified use of "subspecies" is inadvisable where large continuous populations are concerned such as those of many Amazonian forest animals. In these cases subspecific names may refer to clinal forms based on varying subjective criteria or to extensive uniform populations or they may designate highly variable hybrid populations. On the other hand, 'subspecies' are of more direct use in island or montane species where geographic variation is discontinuous and isolated populations are fairly uniform. In any case, analyses of population structure of the species involved should precede or accompany biogeographic studies which use 'subspecies' to establish faunal differences between areas and to interpret the history of their faunas.

²⁾ Locality records based on early commercial collections are mostly reliable or have been corrected in later years. Doubt remains in a few cases where a species is known to inhabit one side of an Amazonian river and isolated early records also place it on the opposite bank, e. g. the records of the southern Amazonian antbird *Phlegopsis nigromaculata* from the north bank of the lower Amazon in Amapá, of the northern Amazonian jacamar *Galbula albirostris* and the antbird *Pithys albifrons* from the Rio Arapiuns near the mouth of the Rio

I constructed distribution maps of Amazon birds by plotting published locality records on base maps prepared from the 1:5,000,000 topographical map of South America (American Geographical Society, 1953). Additional unpublished records of many species were obtained during repeated visits of several museums in the United States, South America and Europe (see Acknowledgements). The resulting distribution maps were compared with the ranges as given by De Schauensee (1966, 1970) in his useful reference lists of South America birds; and a number of the maps have been published (Haffer 1969—1977).

The composite maps accompanying this report (Figs. 2—14) have been prepared in several steps: 1) Individual species maps were divided by visual inspection into several groups composed of species with similar or overlapping distribution (e. g. upper Amazonian, Guianan, etc.). These groups of species are not sharply delimited and the assignment of certain widespread species to a particular species group was necessarily arbitrary ("transitional cases"). 2) Composite maps for each group of species were prepared by superimposing the respective individual species or subspecies maps. This was accomplished by, first, covering Amazonia on the 1:5 million geographical map of the American Geographical Society (1953) with a grid of 1 degree longitude by 1 degree latitude (or approximately 110-km squares), thereby subdividing Amazonia into about 650 grid squares. Secondly, the number of species of a particular distributional group occurring within each grid square was determined. The resulting values were considered as representative for the central portion of each square and were then contoured by isopories (lines of equal numbers of species) to arrive at the composite maps. In this way 'peaks' of species numbers or areas of maximal overlap of breeding ranges of a particular distributional group of species are emphasized and ill-defined range boundaries are deemphasized. The contoured values are the total numbers of species in a particular distributional group per grid square. 3) A composite map (Fig. 15) for the pooled total sample of Amazonian forest birds considered in this study was prepared by superimposing the composite maps of the distributional species groups

Tapajós (for these and other probable errors in labelling bird specimens see Haffer 1974: 108). In addition, several upper Amazonian or central Amazonian species are occasionally listed as occurring in "Cayenne" (or "Oyapock"), although they are not reported from this area except on the basis of old skins purchased from a Paris dealer (Hellmayr in Cory and Hellmayr 1924: 137, 147, footnotes, Hellmayr 1929: 91, footnote), e. g. *Forpus sclateri*, *Touit purpurata*, *Notharchus ordii*, *Pteroglossus flavirostris*, *Selenidera nattereri*, *Celeus grammicus*, *Thamnophilus aethiops*, *Myrmotherula cherriei*, *M. haematonota*, *Myrmeciza pelzelni*, *Heterocercus flavivertex*, *Euphonia rufiventris*. The "Cayenne" specimens of these species may have actually come from the upper Rio Negro region. I have considered these "Cayenne" records as unreliable following Hellmayr (1. c.). This treatment contrasts with that of Novaes (1974) who still lists some of the above species from "Cayenne" or "Oyapock" without comment.

Certain bird specimens collected by members of the Olalla family supposedly in the upper Río Ucayali Valley (eastern Peru), near the mouth of the Río Urubamba, also are suspect and in many cases may have come from the lower Río Ucayali Valley near the Río Marañón, e. g. specimens of the following species from "Lagarto" or "Boca Río Urubamba" in the collections of the American Museum of Natural History, New York: *Pyrhura melanura souancei*, *Pipra erythrocephala*, *Pipra c. coronata*, *Hypocnemoides melanopogon*. This suspicion is based on the fact that the valley of the upper Río Ucayali is inhabited by close relatives of the above forms and no overlap of these species and subspecies pairs is known from other parts of Amazonia (*Pyrhura picta*, *Pipra chloromeros*, *Pipra coronata exquisita*, *Hypocnemoides maculicauda*, respectively).

following a similar procedure: The species numbers for each grid square of the individual maps were totaled and the resulting values were contoured.

Another composite map (Fig. 17) prepared following suggestions by Diamond (1975) illustrates the regional distribution of species range borders in Amazonia. This map was prepared from the tabulated species totals of the 100-kilometer squares by determining the difference of the totals of species inhabiting adjacent grid squares within each species group and combining the resulting figures to arrive at the total number of species borders between adjacent grid squares.

The composite maps constructed following the above method, of course, are generalized because of insufficient knowledge of the outline of individual species ranges and the assumption of continuous (uniform) occurrence of all species within their ranges. Obviously, this is not the case, many species occurring in a rather patchy manner due to unevenly distributed resource levels. Thus, instead of local totals of species numbers the maps illustrate regional totals which may never be reached in any given forest habitat. The distribution of a number of Amazon forest birds certainly will be found to be more extensive than here mapped, thereby "blurring" the distinctness of some of the patterns analysed. However, the group patterns themselves probably will remain unaffected when the analysis is repeated in later years on the basis of a more complete knowledge of faunal and floral distribution in Amazonia. Areas comparatively poorly sampled by collectors to date include southeastern Colombia, the Rio Branco Valley in northern Brazil and the headwater regions of the Tapajós and Xingú Rivers in central Brazil (Haffer 1974, Fig. 7.1).

3. Acknowledgements

I collected background data for the preparation of the composite distribution maps presented in this article over a period of several years while engaged in field work in South America (1957—1967) and during the study of published information and of the skin collections of a number of museums in the United States, South America and Europe. I thank the following curators for access to the collections under their care: D. Amadon, W. Lanyon, L. Short (American Museum of Natural History, New York), F. Gill, R. M. de Schauensee (Academy of Natural Sciences, Philadelphia), M. A. Traylor, E. R. Blake (Field Museum of Natural History, Chicago), K. C. Parkers, M. H. Clench (Carnegie Museum, Pittsburgh), G. Lowery, J. O'Neill (Zoological Museum, Louisiana State University, Baton Rouge), K. Stager (County Museum, Los Angeles), the late A. Olivares (Instituto de Ciencias Naturales, Universidad Nacional, Bogotá), R. A. Paynter, Jr. (Museum of Comparative Zoology, Cambridge), H. E. Wolters (Museum A. Koenig, Bonn), J. Steinbacher (Senckenberg Museum, Frankfurt), J. Reichenhoff (Zoologische Staatssammlung, München), G. Mauersberger (Naturkunde-Museum, Berlin), W. H. Phelps, Jr., R. Avello (Colección Phelps, Caracas), P. E. Vanzolini (Museu de Zoologia, Universidade de São Paulo), H. Sick (Museu Nacional, Rio de Janeiro).

4. Distributional analysis of Amazon forest and forest edge birds

Distribution patterns of Amazonian forest and forest edge birds vary conspicuously despite the continuity and wide expanse of the forests. There are widespread species occupying all of Amazonia and some of

them extended their ranges also to include portions of the neotropical forests west of the Andes and/or in southeastern Brazil. Others are geographically more restricted and occupy only parts of Amazonia. A number of these latter species are surprisingly localized. An explanation of such limited ranges is difficult in the absence of physical barriers in Amazonia (except certain broad river courses) and of information on regionally varying resource levels of the species concerned including the occurrence of potential competitors.

In order to define the basic patterns underlying the immense variety of avian species ranges in Amazonia, I grouped the species and subspecies considered into a number of assemblages based on the geographical similarity or congruence of their ranges. The resulting species groups are not sharply delimited and assignment of certain transitional cases to a particular group remains subjective.

All species of a given group occur together in the variously extensive central portion of the "group area". The number of regionally sympatric species in each group decreases in directions away from the central region resulting in steep to gentle gradients of species totals in several directions. We may envision two alternatives to explain these diversity gradients in the various geographical species groups in Amazonia. Probably a combination of both will be applicable:

- a) *An historical interpretation:* The dispersal distance of the species from a central area of survival/origin decreased away from the center, in some or many cases due to increasing competition with species spreading from other centers.
- b) *An ecological interpretation:* For the species of each group, ecological conditions or resource levels are more favorable in the central portion of their 'group area' leading to the coexistence of a large number of species in a comparatively restricted area; forests change composition as they grade into other forest types away from the center or as they approach savanna regions; rivers and mountains act as differential barriers.

An ecological explanation probably applies to most gradients near the northern and southern margins of the Amazon forest region. The equally conspicuous gradients developed in central portions of Amazonia probably have a strong historical component, as will be discussed below. The basic avifaunal pattern that emerged from this analysis confirmed previous qualitative and less comprehensive interpretations (Haffer 1969, 1974). A set of six restricted distribution centers (core areas) are located in peripheral portions of Amazonia as follows: Napo, Inambari, Imeri, Rondônia, Guiana, and Belém center. We may envision these centers as the geo-

graphic representation of localized species clusters each of them composed of 10 to 50 species. The six clusters together are characterized by a total of around 150 species or about 25 % of the Amazon forest bird fauna. More widespread species characterize increasingly extensive regions which comprise two or more of the above core areas. The regional diversity gradients in each of the groups of species are variously modified by large Amazonian rivers which probably have been of only minor significance for the origin and maintenance of avian species diversity in Amazonia. These topics will be discussed after the presentation of the basic distributional data.

4.1. Widespread Amazonian birds

Among widespread birds restricted to Amazonia there are about 40 species which inhabit most or all forests and/or forest edges of the region (see list below). There are probably many more endemic pan-Amazonian birds but they have been found so far only at widely scattered localities and it would be premature to consider them as occupying all of Amazonia. Two smaller groups of birds (not all of them endemic to Amazonia) are also wide ranging but are missing either from the northeastern or from the southeastern portion of Amazonia. The former group comprises 27 species and subspecies (see list below) which are widespread in upper Amazonia ranging eastward to the upper Rio Negro or into southern Venezuela (Fig. 2). South of the Amazon, most of them reached the Rio Tocantins and over half (i. e. 15 species) continued to the Atlantic coast near the city of Belém. In some cases a competing ally probably prevents the entrance of the western Amazonian form into the Guiana region, e. g. the species of *Celeus*, *Veniliornis*, *Xiphorhynchus*, *Myrmotherula*, *Iodopleura*, *Tyrannutes* and *Euphonia* listed below. The question remains open as to why the other species have not extended their ranges beyond the present limits. The lower Amazon River certainly is a barrier for some species; for several other species the mountainous region of southern Venezuela may represent a barrier zone or they may be held off by diffuse competition.

The 28 widespread species which are missing from portions of the area south of the lower Amazon (Fig. 3) may be hindered in their advance by the wide Amazon River itself or by one of its southern tributaries (Tapajós, Xingú, Tocantins). Potentially competing or hybridizing allies can be identified for only two forms (*Capito dayi* and *Xiphorhynchus eytoni* may prevent the entrance into this region of *C. niger* and *X. guttatus*, respectively).



Fig. 2: Distribution of certain widespread Amazonian birds missing from the Guianan region. Superimposed ranges of 27 species and subspecies (see text for list of names) ¹⁾.



Fig. 3: Distribution of certain widespread Amazonian birds missing from portions of southeastern Amazonia. Superimposed ranges of 28 species and subspecies (see text for list of names).

¹⁾ Only the Amazonian portion of the range of more widely distributed species has been used in the preparation of this and the following maps. Andes mountains above 2000 meters elevation are in black.

Endemic pan-Amazonian species:

<i>Crypturellus cinereus</i>	<i>Philydor ruficaudatus</i>
<i>Crypturellus undulatus</i> (gaps in NE-Amazonia)	<i>Automolus infuscatus</i>
<i>Cathartes melambrotus</i>	<i>Automolus rufipileatus</i>
<i>Daptrius ater</i>	<i>Sclerurus rufigularis</i>
<i>Opisthocomus hoatzin</i> (banks of forest streams)	<i>Myrmotherula longipennis</i>
<i>Ara manilata</i>	<i>Myrmotherula menetriesii</i>
<i>Touit huetii</i>	<i>Cercomacra cinerascens</i>
<i>Caprimulgus nigrescens</i>	<i>Sclateria naevia</i>
<i>Reinarda squamata</i>	<i>Hylophylax poecilonota</i>
<i>Bucco capensis</i>	<i>Corythopsis torquata</i>
<i>Celeus elegans</i>	<i>Cotinga cayana</i>
<i>Melanerpes cruentatus</i>	<i>Attila cinnamomea</i>
<i>Phloeoeastes rubricollis</i>	<i>Platypsaris minor</i>
<i>Dendrocincla merula</i>	<i>Platyrinchus platyrhynchus</i>
<i>Dendrexetastes rufigula</i>	<i>Ramphotrigon ruficauda</i>
<i>Lepidocolaptes albolineatus</i>	<i>Ornithion inermis</i>
<i>Synallaxis propinqua</i> (gap in northern Amazonia)	<i>Atticora fasciata</i> (avoids the Amazon Valley itself)
<i>Synallaxis rutilans</i>	<i>Psarocolius viridis</i>
<i>Philydor pyrrhodes</i>	<i>Paroaria gularis</i> (wet scrub, river borders)
	<i>Tachyphonus surinamus</i>

Widespread species missing from most or all of the Guianan region:

<i>Tinamus guttatus</i>	(?) <i>Cranioleuca gutturata</i>
<i>Leucopternis schistacea</i>	<i>Thamnophilus aethiops</i>
<i>Forpus sclateri</i> (possibly pan-Amazonian)	<i>Thamnophilus schistaceus</i>
<i>Monasa nigrifrons</i>	(?) <i>Pygoptila stellaris</i>
<i>Monasa morphoeus</i>	<i>Myrmotherula hauxwelli</i>
<i>Picumnus aurifrons</i>	<i>Myrmoborus myotherinus</i>
<i>Celeus grammicus</i>	<i>Pachyrhamphus castaneus</i>
<i>Veniliornis affinis</i>	<i>Iodopleura isabellae</i>
<i>Deconychura stictolaema</i>	<i>Tyrannetes stolzmanni</i>
<i>Nasica longirostris</i>	<i>Todirostrum c. chrysocrotaphum</i> group (exclusive <i>T. c. pictum</i>)
<i>Xiphocolaptes promeropirhynchus</i>	<i>Microcerulus marginatus</i>
<i>Xiphorhynchus ocellatus</i>	<i>Hylophilus hypoxanthus</i>
<i>Xenops tenuirostris</i>	<i>Psarocolius yuracares</i>
	<i>Euphonia rufiventris</i>

Widespread species missing from portions of the area south of the lower Amazon River:

<i>Piaya melanogaster</i>	<i>Hypocnemis cantator</i>
<i>Otus watsoni</i>	<i>Pernostola leucostigma</i>
<i>Threnetes leucurus</i>	<i>Myrmeciza atrothorax</i>
<i>Hydropsalis climacocerca</i>	<i>Hylophylax naevia</i>
<i>Capito niger</i>	<i>Myrmothera campanisona</i>
<i>Celeus torquatus</i>	<i>Conopophaga aurita</i>
<i>Xiphorhynchus obsoletus</i>	<i>Neopipo cinnamomea</i>
<i>Xiphorhynchus guttatus</i>	<i>Ochthornis littoralis</i> (river banks)
<i>Xenops milleri</i>	<i>Platyrinchus coronatus</i>
<i>Automolus ochrolaemus</i>	<i>Turdus ignobilis</i>
<i>Thamnophilus murinus</i>	<i>Euphonia chrysopasta</i>
<i>Thamnomanes ardesiacus</i> (including <i>saturninus</i>)	<i>Tangara chilensis</i>
<i>Myrmotherula brachyura</i>	<i>Hemithraupis flavicollis</i>
<i>Myrmoborus leucophrys</i>	<i>Sporophila castaneiventris</i> (clearings in the forest)

4.2. Northern Amazonian birds (Fig. 4)

Fourteen species occur north of the Amazon River from the Andes to the Atlantic coast but are missing from all or most of southern Amazonia. Some of these birds crossed the Río Marañón near the Andes and/or the lower Amazon near its mouth in a southern direction. In this way the northern Amazonian species of *Pionites*, *Pithys*, *Thryothorus*, *Malacoptila* and *Galbula* listed below have followed the base of the Peruvian Andes southward from the upper Marañón River and some of them have reached the upper Río Ucayali Valley in southeastern Peru. The species of *Touit*, *Derophtus*, *Phaethornis*, *Cercomacra*, *Thryothorus* crossed the lower Amazon southward and have occupied variously extensive areas south of the mouth of the Amazon. This river certainly is an effective (yet probably partial) barrier to dispersal for most of these species. In those cases where a competing ally is known to occur on the southern bank (species of *Psophia*, *Leucopternis*, *Pionites*, *Galbula*, *Pipra*, *Lanio*), the range limits probably stabilized along the Amazon to reduce or avoid competition. In the species pair of *Hypocnemoides* the zone of competitive exclusion is located south of the middle and lower Amazon River.

Species list:

<i>Psophia crepitans</i>	<i>Touit purpurata</i>
<i>Leucopternis melanops</i>	<i>Pionites melanocephalus</i>



Fig. 4: Distribution of northern Amazonian birds. Superimposed ranges of 13 species and subspecies (see text for list of names).

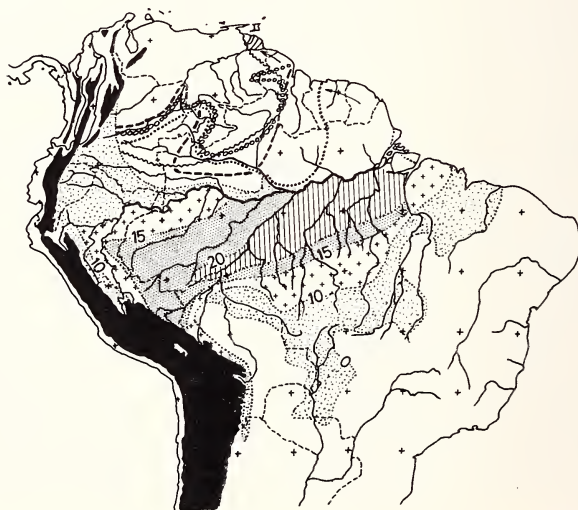


Fig. 5: Distribution of southern Amazonian birds. Superimposed ranges of 21 species and subspecies (see text for list of names). The northern range limits of four more widely distributed species is shown as follows: *Thamnophilus amazonicus* (open circles), *Gymnoderus foetidus* (dashed line), *Todirostrum maculatum* (wiggly line), *Idioptilon zosterops* (dotted line).

*Deroptyus accipitrinus*¹⁾
Phaethornis bourcierii
Malacoptila fusca
Galbula albirostris
Cercomacra tyrannina

Pithys albitrons
*Hypocnemoides melanopogon*²⁾
Pipra erythrocephala
Thryothorus coraya
Lanio fulvus

4.3. Southern Amazonian birds (Fig. 5)

The ranges of 21 species and subspecies are essentially complementary to those of the preceding group, the Amazon River representing the northern range limit in most cases. Several species are the southern geographical representatives of the northern forms (the species of *Leucopternis*, *Pionites*, *Lanio*, *Galbula*, *Hypocnemoides* and *Pipra*). A few species crossed the Río Marañón northward and occupied portions of upper Amazonia near the base of the Andes (the species of *Trogon*, *Electron*, *Malacoptila*, *Xiphorhynchus*, *Myrmotherula*, *Myrmeciza*, *Phlegopsis*, *Campylorhynchus*). *Mitu mitu* is found in a small area north of the Amazon River in southeastern Colombia (Scheuermann, 1977), east of the range of *Mitu salvini*.

Species list:

<i>Crypturellus strigulosus</i>	<i>Xiphorhynchus spixii</i>
<i>Leucopternis kuhli</i>	<i>Xiphorhynchus necopinus</i>
<i>Mitu mitu</i>	<i>Myrmotherula leucophthalma</i>
<i>Trogon curucui</i>	<i>Myrmotherula ornata</i>
<i>Pionites leucogaster</i>	<i>Hypocnemoides maculicauda</i>
<i>Neomorphus g. geoffroyi</i> group	<i>Myrmeciza hemimelaena</i>
<i>Electron platyrrhynchum</i>	<i>Phlegopsis nigromaculata</i>
<i>Malacoptila rufa</i>	<i>Attila bolivianus</i>
<i>Galbula cyanicollis</i>	<i>Pipra rubrocapilla</i>
<i>Picumnus borbae</i>	<i>Campylorhynchus turdinus</i>
	<i>Lanio versicolor</i>

There are seven species which are widespread south of the Amazon and in portions of northern Amazonia: *Dendrexetastes rufigula*, *Microrhopias quixensis*, *Thamnophilus amazonicus*, *Cercomacra nigrescens*, *Todi-rostrum maculatum*, *Idioptilon zosterops*, *Gymnoderus foetidus*. The northern range limits of four of these birds as presently interpreted are shown on Figure 5. All of these species are missing from most of southern

¹⁾ Novaes (1976) collected this parrot along the upper Rio Roosevelt just outside the area mapped as its range here.

²⁾ The range of this species was not included in our map (Fig. 4).

Venezuela. In view of the excellent sampling of this fauna by Phelps & Phelps, Jr. (1958, 1963), these gaps are probably real rather than apparent. We may speculate that the above seven species have spread from southern Amazonia without having yet closed the last gap in southern Venezuela.

4.4. Western Amazonian birds

Among this large group of species we may distinguish widespread species and those that are restricted to northwestern or southwestern Amazonia.



Fig. 6: Distribution of upper Amazonian birds. Superimposed ranges of 77 species and subspecies (see text for list of names).

4.4.1. *Widespread upper Amazonian birds* (Fig. 6). — Seventy species and seven subspecies (or groups of subspecies) are combined in this large cluster of birds. They occur in western Amazonia to the north and south of the Marañón-Solimões River ranging for varying distances eastward into central Amazonia. Several species are restricted to the hilly lowlands near the Andes and many drop out in southeastern Colombia or in the Rio Juruá region of western Brazil. Less than half of the species reach the upper Rio Negro and the Madeira River. One species included here (the guan *Penelope jacquacu*) reached the Atlantic coast in Guyana. The toucan *Ramphastos vitellinus pinto* which is closely allied to the upper Amazonian *R. v. culminatus* ranges into central Brazil (Mato Grosso and

Goιάs). A few of the species have representative populations in the forested lowlands west of the Andes and/or in eastern (lower) Amazonia.

The main pattern observed in this distributional group of upper Amazonian birds is a strong eastward decrease in species numbers from an upper Amazonian center where all or most species coexist in the same general area. Rivers acting as partial barriers to dispersal have modified the steep but fairly smooth eastward gradient of decreasing total number of species within this group. Thus, on the south bank of the Rio Solimões, many species range for a greater distance eastward than on the northern bank. This is shown on the composite map (Fig. 6) by a conspicuous eastward displacement of all contour lines on the south bank of the Amazon River as compared to the northern bank. Other discontinuities or 'steps' in the eastward gradient are caused by the lower Rio Negro and by the Rio Madeira. 18 species reach the western bank of the lower Rio Negro, whereas only 2 to 8 species of this group occur on its eastern bank. By contrast, the upper Rio Negro does not represent any major barrier, the gradient running smoothly across the Vaupés-Guainía region into southern Venezuela. The narrow tongue-like shape of the contour lines of 5, 10 and 20 species in the latter area is produced by the combined barrier effect of the Llanos (grass savannas) to the northwest and the high mountains along the Venezuelan-Brazilian boundary to the southeast.

Species list:

<i>Pulsatrix melanota</i> (Andean foothills)	<i>Pharomachrus pavoninus</i>
<i>Ortalis guttata</i>	<i>Baryphthengus ruficapillus</i>
<i>Penelope jacquacu</i> (excl. <i>P. obscura</i>)	<i>Bucco macrodactylus</i>
<i>Nothocrax urumutum</i>	<i>Monasa flavirostris</i>
<i>Crax globulosa</i>	<i>Capito aurovirens</i>
<i>Anurolimnas castaneiceps</i>	<i>Eubucco richardsoni</i>
<i>Geotrygon saphirina</i>	<i>Pteroglossus inscriptus humboldti</i>
<i>Aratinga weddellii</i>	<i>Ramphastos vitellinus culminatus</i> *
<i>Brotogeris cyanopectera</i>	and <i>pintoii</i>
<i>Pionopsitta barrabandi</i>	<i>Ramphastos tucanus cuvieri</i>
<i>Chordeiles rupestris</i>	<i>Picumnus castelnau</i>
(clearings and river sand banks)	<i>Picumnus rufiventris</i>
<i>Neomorphus geoffroyi aequatorialis</i>	<i>Piculus leucolaemus</i>
(Andean foothills and slopes)	<i>Synallaxis albigularis</i>
<i>Neomorphus pucherani</i>	<i>Metopothrix aurantiacus</i>
<i>Phaethornis hispidus</i>	<i>Hyloctistes subulatus</i>
<i>Eutoxeres condamini</i>	<i>Ancistrops strigilatus</i>
<i>Polyplancta aurescens</i>	<i>Philydor erythropterus</i>
<i>Heliodoxa schreibersii</i>	<i>Automolus dorsalis</i> (near Andes)

Automolus melanopezus
Sclerurus mexicanus
 (upper Amazonian population)
Megastictus margaritatus
Frederickena unduligera
Myrmotherula haematonota
Myrmotherula erythrura
Dichrozona cincta
Terenura humeralis
Cercomacra serva
Thamnistes anabatinus
 (Andean foothills)
Myrmochanes hemileucus
Pernostola schistacea
Myrmeciza hyperythra
Myrmeciza fortis
Phlegopsis erythroptera
Chamaeza nobilis
Conopophaga peruviana
Lioscelis thoracicus
Porphyrolaema porphyrolaema
Cotinga maynana
Cephalopterus ornatus

Schiffornis major
Elaenia gigas (Andean foothills)
Cnipodectes subbrunneus
Tyranniscus gracilipes (excl. *T. acer*)¹⁾
Turdus obsoletus
Turdus lawrencii
Cyanocorax violaceus
Cyphorhinus arada modulator
Clypicterus oseryi
Psarocolius (Ocyalus) latirostris
Psarocolius angustifrons
Cyanerpes nitidus
Dacnis flaviventer
Euphonia xanthogaster
Euphonia lanirostris
Tangara callophrys
Tangara punctata
 (population in Andean foothills)
Tangara schrankii
Tangara xanthogastra
Tangara nigrocincta
Ramphocelus nigrogularis

4.4.2. *Napo forest birds* (Fig. 7). — A group of 38 characteristic species and subspecies is restricted to the northwestern portion of Amazonia centering around eastern Ecuador (and the Río Napo). Five of these species reached the Río Guainía region and only 2 to 4 species entered southern Venezuela. Equally few species crossed the Río Marañón-Solimões southward. This river probably acted as an effective barrier to dispersal for the majority of the species in this group, as shown by the 'truncation' of most contour lines along this river course. Only the contours of 5 and 10 species appear south of the Marañón River, the latter contour line displaced far to the west.

Species list:

Aramides calopterus
 (Napo population)
Mitu salvini
Leucippus chlorocercus

Heliodoxa gularis
Topaza pella (Napo population)
Topaza pyra
Galbula tombacea

¹⁾ Traylor (1977) included this and several related species in the newly defined genus *Zimmerius*.



Fig. 7: Distribution of Napo forest birds. Superimposed ranges of 38 species and subspecies (see text for list of names).



Fig. 8: Distribution of Inambari forest birds. Superimposed ranges of 47 species and subspecies (see text for list of names).

Galbula leucogastra chalthorax
Galbalcyrrhynchus leucotis
Nonnula brunnea
Pteroglossus f. flavirostris
Pteroglossus pluricinctus
Selenidera r. reinwardtii
Celeus spectabilis
 (Napo population)
Synallaxis moesta
Neotantes niger
Myrmotherula sunensis
Myrmotherula obscura
Herpsilochmus sticturus dugandi
Myrmeciza melanocephala
Gymnopathys leucaspis
Grallaria dignissima
Grallaria fulviventeris
 (Napo population)
Attila citriniventeris
Pipra filicauda

Pipra c. coronata group
Heterocercus aurantiivertex
Myiophobus cryptoxanthus
Ramphotrigon fuscicauda
 (Napo population)
Todirostrum c. calopteryx
Todirostrum capitale capitale
Microbates cinereiventris
 (Napo population)
Cacicus sclateri
 Not mapped in Fig. 7 are the
 following species:
Phlogophilus hemileucurus
 (Andean foothills)
Pyrhura albigularis (foothills)
Galbula pastazae (foothills)
Thamnophilus praecox (known only
 from the female type)
Phlegopsis barringeri (known from
 a single locality)

4.4.3. *Inambari forest birds* (Fig. 8). — This group of 47 species and subspecies inhabits the forests of southwestern Amazonia centering in southeastern Peru (region of the Rio Inambari north to the hills in the headwater region of the Rio Purús). A conspicuous gradient of decreasing total number of species within this group is developed in a northern and northeastern direction parallel to the main rivers in this region. 8 to 13 species reached the southern bank of the Rio Solimões without crossing this river. A few species (*Galbula cyanescens*, *Odontophorus stellatus*, *Rhegmatorhina melanosticta*) crossed the Río Marañón and followed the base of the Andes northward entering eastern Ecuador. The Rio Madeira blocked the eastward advance of many species and only four managed to cross it; among them is the Curl-crested Toucan (*Pteroglossus beauharnaesii*) which reached central Brazil. Some of the Napo and Inambari species are geographical representatives.

Species list:

Crypturellus bartletti
Psophia leucoptera
Aramides calopteryx
 (southern disjunct population)
Odontophorus stellatus
Ara couloni (Andean foothills)

Pyrhura rupicola (foothills)
Heliodoxa branickii (foothills)
Phaethornis philippii
Phaethornis stuarti (foothills)
Phlogophilus harterti (foothills)
Malacoptila semicincta

<i>Nonnula sclateri</i>	<i>Grallaria eludens</i>
<i>Nonnula ruficapilla</i>	(known only from type locality)
<i>Galbalcyrrhynchus purusianus</i>	<i>Conioptilon mcilhennyi</i>
<i>Galbula cyanescens</i>	(known from two localities) ¹⁾
<i>Brachygalba albogularis</i>	<i>Pipra chloromeros</i>
<i>Eubucco tucinkae</i> (foothills)	(Andean foothills)
<i>Pteroglossus flavirostris mariae</i>	<i>Pipra coronata exquisita</i> group
<i>Pteroglossus beauharnaesii</i>	<i>Neopelma sulphureiventer</i>
<i>Selenidera reinwardtii langsdorffii</i>	<i>Ramphotrigon fuscicauda</i>
<i>Celeus spectabilis</i>	(southeastern Peruvian population)
(southern disjunct population)	<i>Todirostrum calopterygum pulchellum</i>
<i>Picumnus subtilis</i>	<i>Todirostrum capitale tricolor</i> ²⁾
<i>Simoxenops ucayalae</i> + <i>S. striatus</i>	<i>Hemitriccus flammulatus</i>
(Andean foothills)	<i>Lophotriccus eulophotes</i>
<i>Thamnomanes schistogynus</i>	<i>Idioptilon rufigulare</i> (foothills) ³⁾
<i>Pernostola lophotes</i>	<i>Pipromorpha macconelli</i> (western
<i>Pernostola macrolopha</i>	population near base of Andes)
<i>Myrmeciza goeldii</i>	<i>Microbates cinereiventris</i>
<i>Gymnopithys salvini</i>	(southern disjunct population)
<i>Rhegmatorhina melanosticta</i>	<i>Cacicus koepckeae</i> (known from
<i>Formicarius rufifrons</i>	the type locality)
(known from only one locality)	<i>Tachyphonus rufiventer</i>
	<i>Agelaius xanthophthalmus</i> ⁴⁾

4.5. Central Amazonian birds

This small group of birds is composed of widespread and localized species, the latter being restricted to northcentral and southcentral Amazonia.

4.5.1. *Widespread central Amazonian birds* (Fig. 9). — The following four species are widely distributed in central Amazonia yet have reached neither the Andes in the west nor the Atlantic coast in the east:

<i>Hylophylax punctulata</i>	<i>Snethlagea minor</i>
<i>Phaeotriccus poecilocercus</i> ⁵⁾	<i>Elaenia pelzelni</i>

¹⁾ Previously known only from the type locality at Balta near the upper Purús River. Terborgh (pers. comm.) recently found this species in the Manu National Park, upper Río Madre de Dios, near the base of the Andes.

²⁾ Fitzpatrick (1976) synonymized *T. albilacis* with *tricolor* which he believes is conspecific with the allopatric *T. capitale*. Traylor (1977) united generically *Todirostrum capitale* with *Taeniotriccus andrei* and *Poecilotriccus ruficeps* for which group of species *Poecilotriccus* is the oldest name.

³⁾ Traylor (1977) included the species of *Idioptilon* in the genus *Hemitriccus*.

⁴⁾ Previously known only from the type locality at Tingo Maria. Dr. Terborgh (pers. comm.) discovered this species as common in the small marshes that fringe oxbow lakes in the Manu region of southeastern Peru.

⁵⁾ Included in *Knipolegus* by Traylor (1977).



Fig. 9: Distribution of central Amazonian birds. Superimposed ranges of four species (see text for list of names).

4.5.2. *Imerí forest birds* (Fig. 10). — This group of 15 species is restricted to the upper Río Negro — Río Orinoco region in northcentral Amazonia.

The ranges of several species are confined to the lowlands near the western end of the Sierra Imerí. The Crestless Curassow (*Mitu tomentosa*) has been included in this group, although it is fairly widespread from near the base of the Andes (Sierra Macarena) to the lowlands of northern Guyana. Also included is *Notharchus ordii* which has been found east to Monte Alegre on the northern bank of the lower Amazon.

Species list:

Crypturellus casiquiare

Mitu tomentosa

Notharchus ordii

Selenidera nattereri

Picumnus pumilus

Heterocercus flavivertex

Myrmotherula cherriei

Myrmotherula ambigua

Pernostola caurensis

Herpsilochmus dorsimaculatus

Myrmeciza pelzelni

Cyanocorax heilprini

Dolospingus fringilloides.

Two additional species are known only from their type localities on the upper Río Orinoco:

Tripophaga cherriei

Myrmeciza disjuncta

4.5.3. *Rondônia forest birds* (Fig. 11). — Southcentral Amazonia harbors a number of characteristic birds whose ranges center in the forests between



Fig. 10: Distribution of Imeri forest birds. Superimposed ranges of 15 endemic species (see text for list of names).



Fig. 11: Distribution of Rondônia forest birds. Superimposed ranges of 19 species and subspecies (see text for list of names).

the upper Madeira and Tapajós Rivers. The Rio Madeira, probably acting as an effective barrier, delimits the ranges of many species thereby 'truncating' most of the contour lines. The gradient of decreasing total number of species in this group is more gentle in a northeastern direction but the northward advance of nearly all species of this group is blocked by the lower Amazon River, only one or two species reaching the northern bank.

Species list:

Psophia viridis

Pipile cunjubi nattereri

Pyrhura rhodogaster

Capito dayi

Pteroglossus i. inscriptus

Pteroglossus bitorquatus

Selenidera gouldii

Dendrocolaptes concolor

Dendrocolaptes hoffmannsi

Sakesphorus luctuosus

Myrmotherula sclateri

Myrmotherula assimilis

Myrmotherula iheringi

Rhegmatorhina hoffmannsi

Conopophaga melanogaster

Pipra nattereri

Pipra vilasboasi

Heterocercus linteatus

Odontorchilus cinereus

The following species are known only from the respective type localities:

Idioptilon aenigma

(lower Rio Tapajós)

Todirostrum senex

(lower Rio Madeira)

Myrmeciza stictothorax

(lower Rio Tapajós)

4.6. Eastern Amazonian birds

Among the many species of birds restricted to the eastern part of Amazonia there are again widespread and localized species. The latter comprise a large group of Guianan species and a small group of 'Belém species' which characterize the avifauna south of the mouth of the Amazon.

4.6.1. *Widespread lower Amazonian birds* (Fig. 12). — All of the species in this group occur to the north and to the south of the lower Rio Amazonas extending their ranges for varying distances westward into central or even upper Amazonia. The differential barrier effect of the lower Rio Negro and of the Rio Madeira results in the development of 'stepped' westward gradients, the 'steps' diminishing or disappearing in the headwater regions where the rivers cease to function as barriers. The species which reach western Amazonia are common in lower Amazonia but are rare or of local occurrence in the west such as, e.g., *Galbula dea*. Several species have representative populations in the Atlantic forests of southeastern Brazil.



Fig. 12: Distribution of lower Amazonian forest birds. Superimposed ranges of 21 species and subspecies (see text for list of names).

Species list:

Brotogetis chrysopterus

Polytmus theresiae

Galbula l. leucogastra

Galbula dea

Bucco tamatia

Pteroglossus aracari

Campylorhynchus procurvoides

Hylexetastes perrotii

Sclerurus rufigularis

Sclerurus mexicanus

(lower Amazonian population)

Thamnomanes caesi

(inhabiting most of Amazonia
except southwestern portion where
replaced by *T. schistogynus*)

Grallaria varia

Grallaria macularia

Manacus manacus (inhabiting most of
Amazonia but strangely missing
from large portions of western
Brazil and eastern Peru)

Xenopipo atronitens

Granatellus pelzelni

Hylophilus muscicapinus

Hylophilus pectoralis

Euphonia violacea

Tangara punctata

(lower Amazonian population)

Arremon taciturnus (strangely
absent from the region of the Rio
Solimões and its northern and
southern tributaries; replaced near
the Andes by *A. aurantirostris*)

4.6.2. *Guiana forest birds* (Fig. 13). — This large cluster of 51 species and 8 subspecies renders the avifauna of northeastern Amazonia highly distinctive. All or nearly all of the Guiana species occur regionally together in a comparatively restricted area of the interior of the Guianas.

From this region steep gradients of decreasing total numbers of species within this group run in westerly and southerly directions. Many species circumvent the Roraima mountain massif in the north where the contours form a small westwardly directed 'spur'. The total number of species decreases gradually in southern Venezuela from east to west and a smooth gradient passes through the upper Orinoco — Rio Negro region into eastern Colombia. On the other hand, the lower Rio Negro represents an effective barrier blocking the westward advance of 32 to 14 Guiana species thus truncating in this region the corresponding contour lines. Similarly, the Amazon River prevented the southward spread of most Guiana species. Only 14 species of this species group crossed the river and occupied small areas south of the lower Amazon or of its mouth. These latter species are widespread in the Guiana region and are therefore included in the Guiana species group. The same is true of those few species which reached the upper Solimões or even the base of the Colombian Andes.

Species list:

<i>Ortalis motmot</i>	<i>Colaptes auratus</i> ²⁾
<i>Penelope marail</i>	<i>Contopus albogularis</i>
<i>Crax alector</i>	(hilly areas)
<i>Pionopsitta caica</i>	<i>Todirostrum chrysocrotaphum pictum</i>
<i>Topaza pella</i>	<i>Platyrinchus saturatus</i>
(Guiana population)	<i>Microcochlearius josephinae</i> ³⁾
<i>Monasa atra</i>	<i>Taeniopygia andrei</i> ⁴⁾
<i>Galbula galbula</i>	<i>Tyranniscus acer</i>
<i>Pteroglossus viridis</i>	(possibly conspecific with
<i>Selenidera culik</i>	<i>T. gracilipes</i>)
<i>Ramphastos v. vitellinus</i>	<i>Elaenia ruficeps</i>
<i>Ramphastos t. tucanus</i>	<i>Phylloscartes virescens</i>
<i>Celeus undatus</i>	<i>Pipromorpha macconnelli</i>
<i>Veniliornis cassini</i> ¹⁾	(Guiana population)
<i>Veniliornis sanguineus</i>	<i>Poliophtila guianensis</i>
<i>Xiphorhynchus pardalotus</i>	<i>Cyanocorax cayanus</i>
<i>Frederickena viridis</i>	<i>Cyphorhinus a. arada</i>
<i>Sakesphorus melanothorax</i>	<i>Euphonia plumbea</i>
<i>Myrmotherula guttata</i>	<i>Euphonia cayennensis</i>
<i>Myrmotherula gutturalis</i>	<i>Tangara varia</i>
	<i>Cyanicterus cyanicterus</i>

¹⁾ This species is restricted to northeastern Amazonia; the trans-Andean population represents *V. affinis* rather than *V. cassini* (Short 1974).

²⁾ Included in the genus *Lophotriccus* by Traylor (1977).

³⁾ Included in the genus *Hemitriccus* by Traylor (1977).

⁴⁾ Included in the genus *Poecilatriccus* by Traylor (1977).



Fig. 13: Distribution of Guiana forest birds. Superimposed ranges of 59 species and subspecies (see text for list of names).



Fig. 14: Distribution of Belém forest birds. Superimposed ranges of 10 species and subspecies (see text for list of names).

*Herpsilochmus stictocephalus**Herpsilochmus sticturus*

(Guiana population)

*Terenura spodioptila**Gymnopithys rufigula**Pernostola rufifrons**Myrmeciza ferruginea**Cotinga cotinga**Iodopleura fusca**Phoenicircus carnifex**Pachyramphus surinamus**Haematoderus militaris**Perissocephalus tricolor**Procnias alba**Rupicola rupicola**Pipra serena**Corapipo gutturalis**Neopelma chrysocephalum**Tyranneutes virescens**Periporphyrus erythromelas**Caryothraustes canadensis*

(Guiana population)

Additional species known from

Cayenne should be included here:

*Caprimulgus maculosus**Threnetes niger**Phaethornis malaris*

(also extreme northeastern Brazil)

These species may indicate a separate core area of evolution in the eastern forested parts of the Tumuc-Humac Mountains ('Oyapock' refuge; Brown 1975).

4.6.3. *Belém forest birds* (Fig. 14). — Eight species and 2 subspecies are distinctive elements of the avifauna of the forests to the south of the mouth of the Amazon River. Five forms reached the lower Rio Tapajós and two expanded their ranges to the lower Rio Madeira.

Species list:

*Ortalis superciliaris**Pyrrhura perlata**Aratinga guarouba**Pionopsitta (Gypopsitta) vulturina**Ramphastos vitellinus ariel**Xiphorhynchus eytoni**Conopophaga roberti**Xipholena lamellipennis**Pipra iris**Psarocolius b. bifasciatus*

The following two subspecies might be added:

*Pipile c. cujubi**Brachygalba lugubris naumburgae*

Table 1: Composition of the Amazonian forest and forest edge avifauna

Endemic species		400
Widespread	110	
Local or fairly local	290	
Non-endemic species		250
Also trans-Andean region	81	
Also southeastern Brazil	41	
Also SE-Brazil and trans-Andean region	128	
Total		650

4.7.1. *Total number of species* (Fig. 15). — Avian species inhabiting forests and forest edges in Amazonia total about 650 species (Table 1). A more restrictive count excluding birds of more open edge situations probably would reduce this number to approximately 600 species. About 400 species are restricted (endemic) to Amazonia. The majority of these birds have fairly local distributions despite the continuity of the forests and in many cases two or more species form superspecies in Amazonia. Many other endemic species with more extensive ranges are the Amazonian representatives (allospecies) of more widespread neotropical superspecies with allies in southeastern Brazil and/or in the forests west of the Andes and in Middle America.

The composite map (Fig. 15) of the pooled avian species and subspecies ranges in Amazonia as analysed in previous sections illustrates overall regional patterns. About 200 species which probably inhabit most or all of Amazonia and which have not been considered in the previous analyses should be added to the values as mapped in Figure 15. We therefore count totals of 370—380 species in eastern Ecuador, 350—360 species in south-eastern Peru decreasing to 320 species in the interior Guianas and 300 species near the mouth of the Amazon. This eastward decrease in total number of species by about 20 % may be related in part to an overall eastward decrease of annual precipitation. Ecological factors associated with higher rainfall in upper Amazonia such as, e.g., more luxurious forest



Fig. 15: Distribution of Amazonian forest and forest edge birds. Superimposed ranges of 360 species (see Figures 2—14 and Table 2).

growth and increased plant species diversity, probably explain the maintenance of westwardly somewhat increased numbers of bird species. More numerous and more extensive Quaternary forest refugia in upper Amazonia (as discussed below) may have contributed to a somewhat more intensive speciation in this area.

Except for the Napo center and, more weakly, for the Guiana center, no indications of the Amazonian core areas of distribution are noticeable on the composite map (Fig. 15) suggesting ecological replacement of localized species by other localized or more widespread birds in complementary regions. This results in an overall 'levelling' or ecological adjustment of the total number of avian species in different portions of Amazonia. Additional regional features illustrated by the pooled composite map (Fig. 15) are the barrier effect of the Solimões-Amazon River leading to a conspicuous eastward displacement of the '130' and '150' contour lines on the southern river bank. Only about 110 to 115 species of the sample mapped have been encountered on the opposite northern river bank and less than 100 species of the sample were found in the Rio Branco region north of the lower Rio Negro extending eastward to include the surroundings of Manaus. Slud (1976: 54) also emphasized the low ratios of suboscine: oscine species and of antbirds (Formicariidae): native oscines in these areas, "as though (they) were isolated from the surrounding high levels". Future fieldwork may reduce somewhat this difference, as the Manaus — Rio Branco region has been insufficiently sampled.

The 'tongue-like' northeastern extension of the '130 species' contour line in eastern Colombia illustrates the close distributional relationship of the bird faunas of southwestern Venezuela and of the upper Rio Orinoco — Rio Negro region with that of eastern Ecuador and upper Amazonia in general. The steep gradient of decreasing species numbers mapped in southeastern Colombia may be flattened somewhat if future fieldwork proves the occurrence of some upper Amazonian species in areas farther to the east than presently known.

4.7.2. *Composition of regional avifaunas* (Fig. 16, table 2). — The distributional analysis of the Amazonian bird fauna as outlined in previous chapters revealed several interesting facts. A rather high percentage of upper and lower Amazonian species are endemic elements many of which are restricted-northern (Napo, Guiana) or restricted-southern (Inambari, Belém) in distribution. By contrast, the local endemic elements of the central Amazonian avifauna are much less conspicuous: The central Amazonian avifauna, especially of southern Venezuela, may be interpreted as a composite fauna mostly derived from western and eastern Amazonia. The regionally varying composition of avifaunas is shown along four

transects in eastern, western, northern and southern Amazonia (Fig. 16). The upper Amazonian and Guianan species groups are most conspicuous in their respective distribution areas as are the Napo and Inambari species groups and the species of lower Amazonia. The profiles also illustrate the varying barrier effect of the rivers on distributional patterns.

Table 2: Distributional analysis of 360 Amazonian forest and forest edge birds which are restricted to portions of Amazonia. Approximately 250 additional species inhabit all of Amazonia, although their ranges probably are more or less discontinuous,

	A ¹⁾	B	C	D	E	F	G	H	I	J	K	L	M	Total species
Endemic Amazonian species typical of the respective species group	25	37	15	17	51	8	59	11	12	14	19	21	4	293
Isolated populations of additional 20 endemic Amazonian species typical of the respective species groups ²⁾	11	9	—	2	6	2	5	3	—	—	2	—	—	20
Populations of species not restricted to Amazonia (also occurring in the trans-Andean and/or SE-Brazilian forests)	2	1	—	—	2	—	13	7	2	7	6	7	—	47
Total: Species + (subspecies)	25	37	15	17	51	8	59	11	12	14	19	21	4	293
	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	(13)	(10)	(0)	(2)	(8)	(2)	(18)	(10)	(2)	(7)	(8)	(7)	(0)	67
														360

¹⁾ A — Napo birds. B — Inambari birds. C — Imerí birds. D — Rondônia birds. E — Guiana birds. F — Belém birds. G — Upper Amazonian birds. H — Lower Amazonian birds. I — Northern Amazonian birds. J — Southern Amazonian birds. K — Widespread Amazonian birds missing from the Guianan region. L — Widespread Amazonian birds missing from portions of southeastern Amazonia. M — Central Amazonian birds.

²⁾ Each of these 20 endemic Amazonian species is split in two isolated populations, i. e. a total of 40, which characterize the various distributional groups.

It may be mentioned here that several avian species ranges in Amazonia are insufficiently known to warrant an interpretation. I mention below several examples of birds which are restricted to the forest between the lower Rio Negro and the Rio Solimões: *Amazona (autumnalis) diadema*, *Pteroglossus flavirostris azara*, *Psophia crepitans ochroptera*¹⁾, *Nonnula amaurocephala*. Some of the

¹⁾ Haffer (1974: 107) interpreted this form as a subspecies of the northern Amazonian *P. crepitans* rather than of the southern Amazonian *P. leucoptera*.

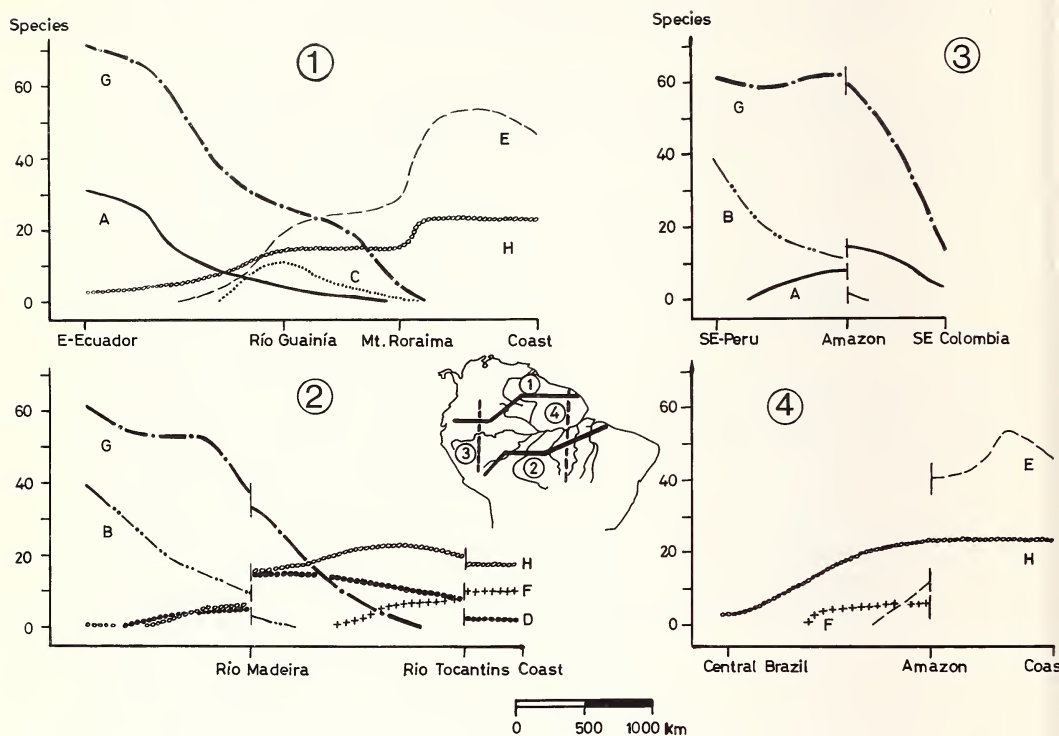


Fig. 16: Main distributional components of the lowland forest avifauna along four transects in Amazonia.

Explanations: Transect 1 — northern Amazonia. 2 — southern Amazonia. 3 — upper Amazonia. 4 — lower Amazonia. A — Napo birds. B — Inambari birds. C — Imeri birds. D — Rondônia birds. E — Guiana birds. F — Belém birds. G — Upper Amazonian birds. H — Lower Amazonian birds. Additional minor components consisting of widespread species are not shown. See index map for location of transects.

subspecies may represent clinal forms of western Amazonian species; the other forms may be more widely distributed than presently known. The same is probably true of the gray forest wren *Thryothorus griseus* which has been collected only along the lower rivers Javarrí, Juruá and Purús in western Brazil. No other bird species is confined to this region. On the other hand, many endemic plants and butterflies led Prance (1973) and Brown (1975, 1977) to postulate at least two forest refuges (Tefé, Loreto) in this part of Amazonia.

Other "special distributional cases" among Amazonian birds include the antbirds *Thamnophilus nigrocinereus*/*T. cryptoleucos* and *Myrmoborus lugubris* which inhabit narrow bands of swampy forests along both sides of the Amazon River and, in the case of the former species, along the Rio Madeira, Ucayali and the Rio Negro into southwestern Venezuela and eastern Colombia. These species avoid the extensive forests at a distance from major rivers. Other birds restricted to the immediate vicinity of the Amazon River and the lower parts of some of its tributaries include *Conirostrum margaritae*, *Cranioleuca muelleri*, and *Myrmotherula klagesi*. The antbirds *Phlegopsis borbae*, *Rhegmatorhina berlepschi*, *R. gymnops* are known only from restricted areas between the southern tributaries of the lower Amazon. These species may have originated on river islands as presently existing or as formed by shifting rivers during past climatic periods (Willis 1969) or they may have originated from populations that were isolated in restricted gallery forests during dry phases far removed from the main Amazonian forest refugia. A further combination generally applicable to Amazonian birds is conceivable: Populations may have differentiated to subspecies level in semi-isolation between large rivers during a humid climatic phase and may have later continued their differentiation to species level in forest refugia during a following arid period.

5. Discussion

5.1. Ornithogeographic significance of Amazonian rivers and mountains

Large rivers delimit, at least for some distance, the ranges of many bird species (Fig. 17), as mentioned in previous sections. We may envision three alternatives to explain this "river effect" depending upon whether the rivers act as absolute or partial barriers to dispersal.

a) Rivers delimit the ranges of species which are unable to cross or circumvent the watercourse. I mention as examples some birds of the dark forest interior which occupy only the southern side of the lower Amazon River despite the apparent absence of potentially competing representatives on the opposite river bank: the ground-cuckoo *Neomorphus geoffroyi* and the manakins *Pipra nattereri* and *P. iris* are widespread south of the lower Amazon. Their northern representative allies *N. rutipennis* and *P. serena*, respectively, are confined to the mountainous region at some distance to the north of the Amazon thus leaving the lowlands along the northern bank of this river uninhabited by either of these species (see

distribution maps by Haffer 1970, Fig. 15 and Haffer 1977a, Fig. 1, respectively). Many other birds for which the lower Amazon is the range boundary may be unable to cross this river, although it is often difficult to rule out the possibility of a competing ally preventing the range expansion (see below).

b) Rivers as partial barriers to dispersal stabilized the equilibrium between competing species or between hybridizing subspecies, in the latter case drastically reducing gene flow. In other words, the birds under consideration would probably cross the river or circumvent it in the headwater region but for the existence there of a competing or hybridizing ally. This interpretation probably applies to many representative bird species occupying the northern and southern banks of the lower Amazon River, e.g. species of *Pionites*, *Selenidera*, *Pteroglossus*, *Xipholena*, *Euphonia* as well as the potentially hybridizing toucans *Ramphastos v. vitellinus* and *R. v. ariel* and the hybridizing subspecies *R. t. tucanus* and *R. t. cuvieri* (see Haffer 1974, 1977b for details). The manakin *Pipra nattereri* occurs only on the west bank of the wide lower Rio Tapajós but, in the headwater region of this river, has extended its range far to the east. The bird's further advance in circumventing the Tapajós River was, however, blocked by competing allies found on the eastern bank of the Tapajós (*P. vilasboasi*, *P. iris*; see distribution maps in Haffer, 1970).

c) Diffuse competition with more distantly related forms and/or somewhat different ecological conditions on the opposite river bank may prevent the spread of certain species despite the fact that a "bridge head" has been formed in some cases. A possible example is the Olive Oropendola (*Gymnostinops yuracares*)¹⁾ which occurs in all of upper Amazonia ranging to the northern bank of the lower Amazon and to southwestern Venezuela. However, it is missing from all of northeastern Amazonia for no obvious reasons²⁾.

The above discussion emphasizes the probability that in many cases interspecific competition rather than inability to cross the watercourse determines species range borders to coincide with a river in Amazonia. However, proof for this statement will be difficult to furnish. The comparatively small differences in total number of species on opposite banks of the Amazon River, as shown in the sample mapped in Fig. 15, may be due

¹⁾ Haffer (1974: 80) considers this form as conspecific with *G. bifasciatus*, since both hybridize freely in southeastern Amazonia. *Gymnostinops* has been merged with *Psarocolius* by Blake (1968).

²⁾ Another example cited by Haffer (1974: 107), the antthrush *Phlegopsis nigromaculata* which is widespread south of the Amazon River, is probably not valid, as the specimens supposedly "from the north bank of this river in Amapá" may have been mislabelled.

to the inability of some species to cross this river. However, in many or most cases where species range borders coincide with the Amazon, the lower Rio Negro, the Rio Madeira or the lower Rio Tocantins (Fig. 17), ecological replacement and competitive interactions between species occupying opposite banks probably are the determining factors. Detailed studies of populations on opposite river banks in areas where islands might facilitate river crossings would be of great interest.



Fig. 17: Avian species range borders in Amazonia. Data derived from sample of 360 species maps. Solid circles illustrate varying numbers of species range borders along the Amazon and its major tributaries (see scale). Stippled areas have less than 10 species range borders per 100 kilometers distance. Two additional stippled contour lines in northern Amazonia indicate 20 and 30 species range borders per 100 kilometers distance. The increasingly crowded contours approaching the northern and southern limits of the Amazonian forest are not mapped.

Dashed line follows zero contour of total sample (Fig. 15).

The ratio of species range borders per 100 kilometers distance is usually less than 10—15 in Amazonia (Fig. 17). However, the cumulative total of species borders away from the rivers is much larger than the local clusters of species borders along these water courses. An exception is the region of the wide lower Rio Amazonas which seems to be a formidable barrier zone for many birds (but not for those here designated 'lower Amazonian' in distribution; see Fig. 12 and Fig. 16, transect 4).

The composite maps (Fig. 2 to 15) and the transect profiles (Fig. 16) illustrate the changing ratio of species range borders per unit distance over the Amazonian lowlands. These gradients certainly are independent of the rivers, although 'broken' (displaced) or locally modified by the water courses.

In northern Amazonia, the mountain ranges along the Brazil/Venezuela boundary (Sierra Imerí, Parima, Pacaraima, Roraima) represent a major barrier zone where range borders are clustered (Fig. 17). Areas to the east and west of these mountains and between major Amazonian rivers are characterized by low indexes of range borders per unit distance, e. g. the Napo region in upper Amazonia, northeastern Amazonia (Guianas), and the lowland between the Ucayali, Madeira, Tapajós and Tocantins Rivers, respectively. This pattern as derived from a consideration of a composite of all range borders of our sample of 360 species should not be used in an historical interpretation, as the pattern is primarily determined by wide ranging species. Inspection of our Figures 2 to 5 indicates that most of the range borders along major rivers are those of species occupying large portions of Amazonia and which have extended their ranges considerably from their center(s) of origin or survival. The approach of a more detailed analyses of distribution patterns to delineate evolutionary 'distribution centers' appears to yield more meaningful results for an historical interpretation.

5.2 Distribution centers and forest refugia

A significant result of the above distributional analysis is that few (only six) localized avian distribution centers exist in the Amazonian lowlands around which 25 % of the Amazonian bird species cluster¹⁾. Judging by the number of species involved, the Guiana center today is most strongly characterized followed by the Napo and Inambari centers. The other three centers are more weakly defined, as they are determined by only about 10 to 15 species each. These areas of increased numbers of localized species are developed in peripheral portions of Amazonia near the base of the Andes, of the Sierra Imerí, of the central Brazilian tableland and of the Guiana highlands. Historically, the distribution

¹⁾ I exclude avian distribution centers in the montane forests along the slopes of the table mountains of southern Venezuela and along the eastern slopes of the Andes. Several species and well differentiated subspecies are restricted to the Huallaga Valley in eastern Peru which may be designated an Andean lowland center: *Pyrhura (melanura) berlepschi*, *Brotoyeris cyanoptera gustavi*, *Ramphocelus melanogaster*. Additional large core areas exist in the trans-Andean lowlands and in southeastern Brazil which, however, are outside the scope of this article (see Müller 1973, Haffer 1974, Brown 1975, 1977).

centers may indicate the general location of Quaternary forest refugia especially when evidence derived from the location of secondary contact zones in various groups of animals in Amazonia and from palynological, pedological and geomorphological studies is also taken into consideration (Haffer 1969, 1974, 1978; Brown 1975, 1977; Simpson & Haffer 1978). The general locations of forest refugia independently reconstructed on the basis of geomorphological and climatological data correlate rather well with the locations of refugia based on biogeographical data alone thus supporting the above historical interpretation. This analysis indicates that probably only six major forest refugia or groups of refugia have been of importance for avian differentiation during the Quaternary. Certainly many more remnant forests existed and have acted as refugia for the forest fauna during the peaks of arid phases. However, their bird populations may have been too small to survive or to contribute significantly to the differentiation process of the avifauna. The Tertiary island theory mentioned in the introductory section most probably is applicable to the early differentiation of ancestral groups of extant families and genera of birds. The drastic environmental changes during the Quaternary led to more recent processes of speciation and subspeciation. The distributional contour maps (Figs. 2 to 15) illustrate the fact that regional gradients of decreasing species totals within the various species groups and around the distribution centres are mostly independent of river courses which merely modify basic patterns locally.

In the areas between adjacent distribution centers, some of the species of one species group are replaced along secondary contact zones by competing or hybridizing allies of neighboring groups (Haffer 1970, 1974). The explanation would be that these previously separated populations have met in the recent geological past. Such cases support the interpretation that the gradients of species numbers around core areas are at least partly explained historically by varying dispersal distances of species from the core areas which have acted as past centers of survival and/or differentiation. In many other geographically restricted species, competitors or varying ecological conditions which delimit the distribution remain unrecognized.

The forest refugia of the Amazonian biota during dry climatic phases of the Quaternary as reconstructed for various groups of organisms on the basis of biogeographical, palynological, geomorphological and climatological data show many correlations but also some differences especially regarding the number and size of the refuges (see reviews by Brown 1975, Haffer 1978). A few large refugia have been of importance for birds and lizards contrasting with the situation in insects and plants for which more numerous refugia of varying size (large to small) have been analysed. The

latter groups may have survived in smaller remnant forests than birds, reptiles and mammals of which, on the average, only larger populations may have survived in the main blocks of forest. The Amazonian 'dispersal centers' described by Müller (1973) are generalized and show basic correlation with the reconstructed forest refugia¹⁾. More geomorphological and palynological data from Amazonia are needed to place the discussion of Quaternary forest refugia on a broader geoscientific basis.

It will be interesting to analyse evolution, adaptation and extinction of animal populations during their isolation in the ecological islands of the refugia. Interruption of gene flow in connection with genetic changes under differing climates and varying competitive situations in the refugia probably led to rapid divergence of many bird populations. On the other hand, disorderly extinction of species in the various refugia rather than interruption of gene flow may have been the force for adaptive changes of races in mimicking *Heliconius* butterflies (Turner 1977).

In an interesting application of the biological model of faunal differentiation to the human occupation of Amazonia, Meggers (1975, 1977) correlated aspects of cultural distributions and migrations of Indian tribes with environmental changes based on linguistic, ethnographical and archeological data. Pre-historic man had arrived in South America probably early enough to have experienced extensive climatic-vegetational fluctuations in Amazonia during the late Pleistocene and Holocene (MacNeish 1976). In several South American countries, the recently published maps of postulated Quaternary forest refugia have shaped proposals for forest reserves. As Brown (1977) has pointed out, not only should forests containing maximum species diversities be preserved but also portions of interrefugial forests where secondary contact zones are clustered permitting future studies on the genetics and ecology of hybridizing and parapatric non-hybridizing forms.

6. Summary

A quantitative analysis of avian distribution patterns in Amazonia indicates the existence of only six distribution centers ('core areas') in this forest region: Napo and Inambari centers in western Amazonia, Guiana and Belém centers in eastern Amazonia and Imeri and Rondônia centers in central Amazonia. These

¹⁾ Müller (1973) based his analysis mostly on ornithogeographical data but gave no details of his method to delimit 'dispersal centers', especially where these are extensive and separated by narrow 'corridors', hence a discussion is not feasible. A comparison with our maps show that the boundaries of Müller's "centers" rarely coincide with those of avifaunal core areas. Usually the boundaries as established by Müller fall in the peripheral gradient of decreasing species totals or coincide with river barriers.

centers are characterized by 10 to 55 species and subspecies each. The majority of Amazonian forest and forest edge birds belong to groups of species which are more widely distributed, their ranges comprising two or more core areas.

The barrier effect of large rivers is not conspicuous in the avifauna as a whole, modifying to some extent the regional eastward gradient of decreasing total number of species in Amazonia. The barrier effect is more pronounced in the case of the lower Amazon River and of individual core areas but also here the rivers act as differential barriers merely modifying the gradients of decreasing species numbers around the distribution centers. Rivers often separate the ranges of close allies for some distance. Under these conditions, competition is diminished or avoided.

Core areas probably indicate the general location of major forest refugia during dry climatic periods of the Quaternary. Amazonian species and subspecies of birds and other animals survived or originated in these refugia during adverse environmental phases. Refugia postulated for birds, reptiles, insects and plants show conspicuous correlations but differ in number and size. Additional geomorphological and palynological studies in Amazonia are required to substantiate more fully these biological interpretations.

7. Zusammenfassung

Verbreitung der Waldvögel Amazoniens. — Eine quantitative Areal-Analyse der Waldvögel Amazoniens ergab als Grundmuster 6 Verbreitungszentren ('core areas'): das Napo, Inambari, Imeri, Rondônia, Guiana, und Belém Zentrum, von denen jedes durch 10—55 Arten und Unterarten charakterisiert ist. Die Mehrzahl amazonischer Waldvögel gehört jedoch zu Gruppen von Arten, deren Verbreitungsgebiete zwei oder mehrere dieser Zentren umfassen. Darunter sind oberamazonische und unteramazonische Arten besonders zahlreich.

Die Schrankenwirkung der Flüsse Amazoniens war für die Entstehung und Ausbreitung amazonischer Waldvögel insgesamt wahrscheinlich von nur untergeordneter Bedeutung, obwohl Flüsse heute die Arealgrenze zahlreicher Arten und Unterarten bilden. Die graduelle Abnahme der Gesamt-Artenzahl der Avifauna von West nach Ost wird durch breite Ströme nur lokal modifiziert. Im Falle individueller Verbreitungszentren ist die differentielle Schrankenwirkung einiger Flüsse auffällig. Aber auch hier werden bestehende Gradienten abnehmender Artenzahlen um die Zentren durch Fluß-Barrieren nur modifiziert. Breite Flüsse trennen häufig die Verbreitungsgebiete konkurrierender (parapatrischer) Arten und hybridisierender Unterarten, dadurch ein labiles Gleichgewicht stabilisierend. In diesen Fällen sind die Flüsse partielle Ausbreitungsschranken.

Historisch interpretiert deuten die Verbreitungszentren die ungefähre Lage größerer Rest-Wälder an, die während trockener Klimaperioden des Quartär in Amazonien erhalten blieben und der Waldfauna als 'Refugien' dienten. Hier überlebten früher existierende amazonische Vogelarten der Regenwälder ungünstige Klima-Perioden oder starben aus oder wurden während der Isolation als Subspezies bzw. als neue Arten differenziert. Diese Formen erweiterten ihr Areal beim Vordringen der Wälder unter feuchterem Klima und trafen dadurch mit den oft ebenfalls differenzierten Populationen anderer Refugien zusammen. Verbreitungszentren in Amazonien, die aufgrund biogeographischer Daten unabhängig für Vögel, Reptilien, Insekten und Pflanzen rekonstruiert wurden, sind auffällig

korreliert, aber zeigen Unterschiede in bezug auf Anzahl und Größe. Diese biologischen Interpretationen sind durch weitere geomorphologische und palynologische Untersuchungen in Amazonien abzusichern.

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Address of author: Dr. J. Haffer, Meisenburgstr. 15, D 4300 Essen.

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