ZOOGEOGRAPHICAL NOTES ON THE «NONFOREST» LOWLAND BIRD FAUNAS OF NORTHWESTERN SOUTH AMERICA

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I. INTRODUCTION

The two major ecological formations found in the tropical lowlands of South America are "forests" and "nonforest" vegetation. Both cover immense terrain and are inhabited by faunas of widely different aspect with numerous species confined to each. The differentiation of these faunas at the species and subspecies level was probably appreciably influenced by the climatic history of the Pleistocene and post-Pleistocene. The forests were contracted during dry periods and expanded during humid climatic periods, resulting respectively in an areal expansion and contraction of the nonforest vegetation.

In this article the history and zoogeographic relations of the faunas inhabiting the nonforest regions of northwestern South America will be considered. The term "nonforest" is here rather broadly defined to comprise open areas, such as grassland savannas, open dry woodland, cactus wastes, thorn scrub, etc. The distinction of such "open" and "forested" areas is rather artificial, particularly in transitional regions of wooded savannas to light deciduous forests and in areas where man has cut the forest recently.

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II. DISTRIBUTION OF NON-FOREST REGIONS IN SOUTH AMERICA

Very extensive areas of central and northeastern Brazil are occupied by cerrado, campos cerrados, campos sujos, campos limpos and caatinga. These types of vegetation comprise a sequence of semideciduous woods and dense scrub to open grassland and thorn forest to cacti scrub, respectively. Today they separate the Amazonian forest from the forest of southeastern Brazil almost completely, as they stretch from the base of the Andes in Bolivia to the Atlantic coast. The northern limit is ill defined. Tongues of open campos reach far north into the Amazonian basin, and the forests extend southward as gallery forests far into the campos region of central Brazil. Isolated campos, surrounded on

all sides by forest, are found within the Amazon valley. Their number and
exact distribution cannot yet be indicated accurately and the accompanying
map (Fig. 1) gives only a first approximation. The isolated campos within
the Amazonian forest are here shown as described by Hueck (1966). A large
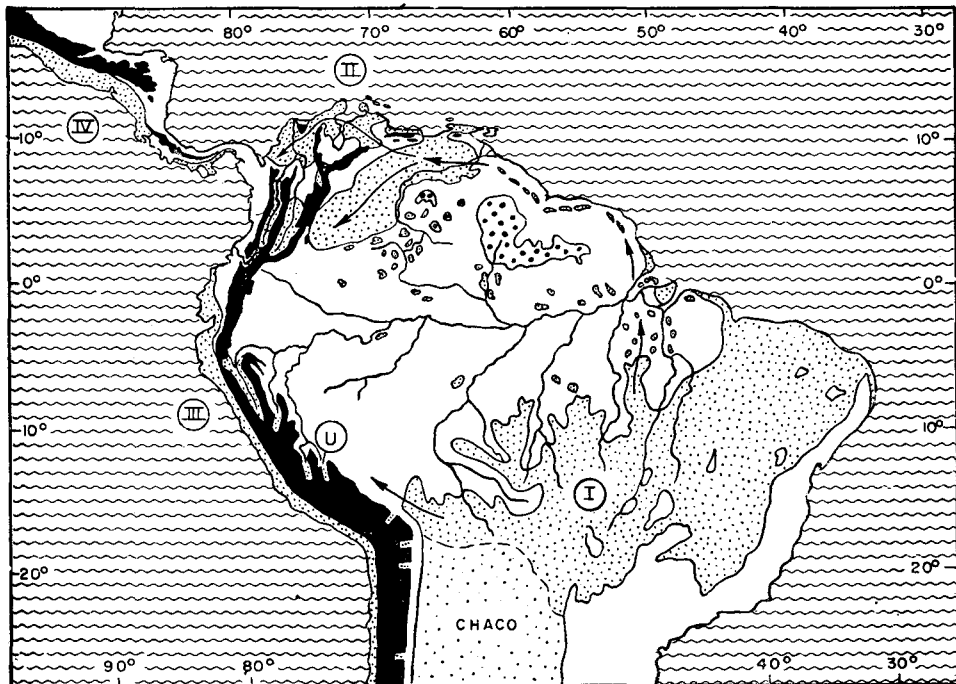

Fig. 1. — Present distribution of nonforest vegetation in tropical South and Central America
    (after Hueck 1960 and 1966, Lauer 1959). Elevations over 1000 meters are in black.
Key : dotted areas — cerrado, campos and caatinga south of the Amazon river; chaparral and
    savannas of northern South and Central America with gallery forests and/or small patches
    of deciduous woods. Semidesert and desert along the Pacific coast of South America. The
    savannas of the Guiana table mountains and of part of the surrounding lowlands are heavily
    dotted. Blank areas — forest. Arrows indicate advancing nonforest faunas during dry climatic
    periods of the Pleistocene and post-Pleistocene.
U, Urubamba valley ; I, Brazilian nonforest region ; II, Colombian-Venezuelan nonforest region ;
    III, Arid Pacific coast region ; IV, Central American nonforest region.
Note: the campos just north of the lower Amazon river are more extensive than indicated on the map.

number of extensive campos occur in the lower Amazon valley; they are
much rarer in the upper Amazon region. Continuing northward we encount-
er savannas in the coastal lowlands of the Guianas (Bakker 1954) and isolated
campos in the upper Orinoco region (Hueck 1960) and in the upper Rio
Branco valley. The high savannas of the table mountains of the Roraima massif
and those farther east (Mt. Duida, etc.) do not belong in this category as
they occur at elevations ranging from 2000 to 3000 meters and are inhabited
by a different fauna.

Extensive savannas are found in the Caribbean lowlands of northern South America; these are immense grass plains with only limited growth of trees along the rivers. The open plains of the lower Rio Orinoco and of the Rio Meta stretch from the Atlantic Ocean westward to the Andes, where, however, the foot and the slopes of the mountains are covered with forests (which are partially destroyed today). The narrow coastal lowlands of Venezuela, including the Peninsulas Paraguaná and Goajira, are covered with cactus wastes
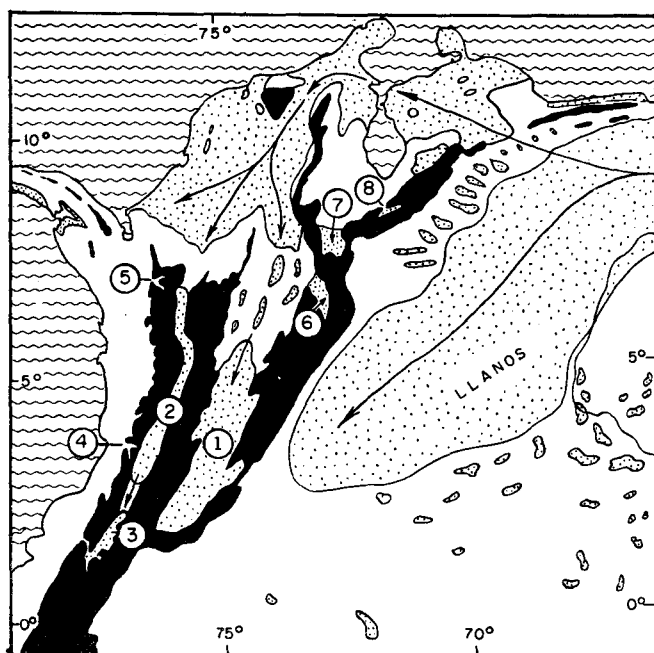

Fig. 2. — Nonforest areas of northwestern South America (adapted from Chapman 1917, Hueck 1960, and author's observations in Colombia). Elevations over 1000 meters are in black. Arrows indicate advancing nonforest faunas.

Key : dotted — nonforest areas ; blank -- forest ; the dry inter-Andean valleys are numbered as follows : 1 Upper Magdalena valley, 2 Cauca valley, 3 Upper Patía valley, 4 Dagua valley, 5 Dabeiba valley, 6 Chicamocha valley, 7 Cúcuta valley, 8 Chama valley.

Note : Low flat-topped mountains covered with nonforest vegetation are more numerous in Amazonian Colombia than shown on the map.

and thorn scrub. The same is true for parts of the country near the mouth of the Rio Magdalena in northern Colombia. However, most of the lowlands of northern Colombia are covered today with extensive grasslands and cultivated savannas along the lower rivers Sinú, San Jorge, Cauca and Magdalena.

The bases of the Andean mountain ranges are mostly forested as the moisture laden winds are sharply cooled by the steep slopes, which results in frequent rainfall. This is the reason for the occurrence of isolated humid forests within the dry Caribbean lowlands of Colombia at the northern foot

of the Sierra Nevada de Santa Marta, in the Serranía de San Jacinto and on the coastal Cordilleras of Venezuela.

Deep intermontane valleys of the Andes are mostly dry and devoid of heavy forest, as the humidity is caught by the surrounding mountains. The cool winds which blow down daily into these valleys from the highlands have an additional desiccating effect as they are warmed up in the lower tropical elevations. We often find thorn scrub and cacti or xerophytic deciduous forests as the only vegetation in these valleys. The upper Magdalena, Cauca and Patía valleys of Colombia are the largest of these intermontane valleys of the northern Andes. They are located between the three main Andean ranges of Colombia. Smaller dry valleys of some importance in this area are those of the Rios Dagua, Dabeiba, Chicamocha, Zulia and Chama (Fig. 2). Large dry inter-Andean valleys are also found in the Peruvian and Bolivian Andes, i.e. the valleys of the upper Rios Marañón, Urubamba, La Paz, Rio Grande, Pilcomayo, etc.

The lowlands along the Pacific coast of South and Central America are mostly open and dry except for the heavily forested lowlands of western Colombia and those of southwestern Costa Rica. In northern Chile, Perú and southwestern Ecuador the cold antarctic waters of the Humboldt current lower the average temperature of the sea winds, which are warmed up upon reaching the adjoining land. This results in a pronounced lack of precipitation. The dry Central American lowlands of the Pacific slope are located in the rain shadow of the moisture laden winds, which blow mainly from the northeast.

III. PLEISTOCENE AND POST-PLEISTOCENE CLIMATIC HISTORY OF TROPICAL SOUTH AMERICA

The details of the climatic history of northern South America, as far as known today, have been given in a recent publication (Haffer 1967). The major points are briefly summarized below. The refrigeration of the climate during the glacial periods of the Pleistocene was not strong enough to seriously affect the faunas of the tropical lowlands. However, there was expansion and contraction of the equatorial rainbelt during the wet glacials and the dry interglacials respectively, particularly affecting the marginal Tropics. Similarly alternating dry and wet periods continued throughout the post-Pleistocene. These climatic changes resulted in a corresponding expansion and contraction of forests in the tropics of South America. It seems probable that the Brazilian campos extended farther north during dry climatic periods, but were pushed somewhat to the south of their present limit during humid climatic periods. The forests of northern South and Central America were probably restricted to several isolated refuge areas during the dry periods, and were broadly connected during wet periods.

The changing distribution of the forest and nonforest vegetation probably caused the repeated isolation and consequently allowed the differentiation of many bird populations. The latter often came in secondary contact with their parent populations when a connection of their habitats had again been established during a later climatic period.

IV. NONFOREST FAUNAS OF SOUTH AMERICA

1. THE BRAZILIAN NONFOREST FAUNA.

The faunal assemblage here designated as the "Brazilian nonforest fauna" inhabits the extensive central Brazilian tableland of relatively dry and open cerrado * and campos. It also comprises the faunas of the dry Chaco, the savanna country of eastern Bolivia and the northeast Brazilian caatinga region. A detailed analysis would certainly result in a subdivision of the above assemblage. which was united for the present purpose of comparing it as a whole with the nonforest faunas to the north and northwest.

The Brazilian nonforest fauna inhabits the greater part of the Brazilian Shield, a geologically very old land mass which was above sea-level at least during most of the Tertiary. The vegetation cover and its fauna also seem old, for numerous endemic species are present. This suggests a long and independent evolution (Sick 1963, 1965). It has been claimed that the vegetation of the large campos region were caused by fires set by the early human inhabitants of these areas. However, this theory has been refuted repeatedly (Cole 1960, Hueck 1966 : 268, Sick 1965).

The nonforest faunas of northwestern South America probably were derived to a large extent from the Brazilian nonforest fauna. The relations of these faunas with that of central Brazil will be discussed below.

2. THE COLOMBIAN-VENEZUELAN NONFOREST FAUNA.

The Colombian-Venezuelan nonforest fauna inhabits the extensive grassland savannas of Venezuela north of the Rio Orinoco and in eastern Colombia ("Llanos"). It also occupies the Caribbean lowlands of northern Venezuela and northern Colombia (Caribbean Fauna of Chapman, 1917) and has advanced in a southern direction into the deep valleys separating the three Andean ranges of Colombia. The savanna fauna of the Guianas should probably also be included here.

The climate of these areas is strongly influenced by the trade winds, which

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* In places the cerrado approaches ecologically a light forest, and a large proportion of its characteristic bird species are arboreal (Sick 1966). However, in its typical form the cerrado still is a "nonforest" vegetation type (but should not be classified as a "savanna").

blow during the dry season from December to March. They cause a very arid climate along the Caribbean coast, where the lowlands are covered only with scattered cacti and thorn scrub grading backward into xerophytic thorn forest. In the savannas of the Rio Orinoco and Rio Meta the climate is somewhat more humid, although the trade winds are still strongly felt during the dry season. It should be noted that the southwestwardly extending grasslands of eastern Colombia are located in the path of these regular winds, which may have been an important factor for the development of these unforested plains.

A subdivision of the area inhabited by the Colombian-Venezuelan nonforest fauna into three subregions would be possible on the basis of certain species and/or subspecies restricted to each. These areas are the highly arid Caribbean coast including the Guajira and Paraguaná Peninsulas, the savannas east and west of the northern Andes, and the dry intermontane valleys of the Colombian Andes. The species and subspecies confined to the arid Caribbean coast are *Leucippus fallax, Inezia tenuirostris, Pyrrhuloxia phoenicea, Arremon tocuyensis, Thraupis sayaca glaucocolpa, Poecilurus candei, Hypnelus ruficollis decolor, Centurus rubricapillus paraguanae, Synallaxis albescens perpallida* and *Sakesphorus canadensis phainoleucus* (Barnes & Phelps, 1940, Haffer, 1961, Todd & Carriker, 1922). The following species do not occur beyond the arid Guajira Peninsula in northern Colombia, but have a somewhat wider ecological range east of the Andes, where they range south into the Orinoco and Meta plains: *Columba corensis, Scardafella squammata, Aratinga acuticauda, Icterus icterus* and *Saltator orenocensis*.

The endemic forms of the Andean valleys are listed in the Appendix and are discussed beyond.

A distributional analysis of 101 characteristic species of the Colombian-Venezuelan nonforest fauna, excluding all water and swamp birds, is given below (for a detailed list of the species concerned see the Appendix). The data for distribution were drawn from the regional catalogues by Phelps & Phelps, Jr. (1958, 1963), de Schauensee (1948-1952, 1964, 1966) and Eisenmann (1955):

Species confined to the lowlands east of the Andes   11
     Brazilian forms, undifferentiated   3
     Subspecies of Brazilian species   4
     Endemic species   4
Species advancing into the Caribbean lowlands of northern Colombia, but not reaching the inter-Andean valleys   33
     Subspecies of Brazilian especies   17
     Endemic species   16
Species reaching the Caribbean lowlands and also advancing into the inter-Andean valleys of Colombia   57
     Subspecies of Brazilian species   35

Endemic species......................................	16
Subspecies of Central American species	5
Subspecies of Chocó species	1
26 reach only the upper Magdalena valley (13 endemic subspecies) ; 28 advance both into the upper Magdalena valley (8 endemic forms) and into the Cauca-Patía valley (12 endemic subspecies) ; 3 advance only into the Cauca-Patía valley (2 endemic forms).	

<div align="right">

Total.............. 101

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The salient features of the above analysis are : the almost complete lack of endemic genera *, the comparatively low number of endemic species and the close relationship of most birds with species of the Brazilian nonforest fauna. Moreover, among the endemic species some are merely strongly differentiated representatives of Brazilian species.

Twelve species of the Colombian-Venezuelan nonforest fauna are confined to the lowlands east of the Andes. Out of a total of 91 species which reached the north-Colombian plains 54 advanced southward into the Magdalena valley, 31 into the Cauca-Patía valley and 46 species reached Central America. Some of the Middle American populations are today quite distinct from the Colombian population and are considered as separate species (see Appendix). Only 6 nonforest species of this sample seem to have entered northern South America from Central America.

The fauna of the intermontane valleys of the Colombian Andes

1. The Upper Magdalena valley.

The dry upper part of the Magdalena valley from about La Dorada to the south is separated from the open Caribbean lowlands of northern Colombia by a Moist Tropical Forest, which covers the humid central part of the valley. The southern arid portion is the largest of the dry intermontane valleys of Colombia, consequently its fauna is the richest. The avifauna has been discussed in considerable detail by A. H. Miller (1947, 1952) and only a few important facts are briefly summarized below. The relations with the Caribbean lowlands are very close; all of the 54 typical species have probably reached the valley from the north and 33 are not even subspecifically distinct, while 21 are recognized as different forms. There are no endemic species (except perhaps *Euphonia concinna,* which may be a representative of *E. trinitatis* of northern Colombia). A few species range throughout the entire length of the Magdalena valley and inhabit the upper arid region as a clinal form,

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* *Hypnelus* and *Quiscalus* appear to be the only ones. The monotypic genus *Gymnomystax* is not fully characteristic, as it is also found along rivers of the entire Amazon basin.

e.g. *Manacus manacus flaveolus*. Another example is *Nystalus radiatus*, a species hitherto considered monotypic and not known from the upper Magdalena valley. This seems to be the only Chocó element which extended its range south into the arid portion of the valley.

The collections of the Instituto de Ciencias Naturales (Universidad Nacional) in Bogotá contain six females of *N. radiatus* from the region of Carmen de Apicalá and Melgar, Dep. Tolima, southeast of Girardot and within the dry upper Magdalena valley. These specimens are pure white and buffy white below, particularly on the throat and lower abdomen; the nuchal collar is buffy to whitish-buffy. This pale population should be separated nomenclaturally from the more richly colored form inhabiting the Pacific lowlands west of the Andes and ranging into Panamá and through the lower Cauca and the humid middle Magdalena valley. Intermediate specimens are known from around Honda in the transition zone of the humid and the arid sections of the Magdalena valley (Chapman, 1917 : 342). An intermediate female from Victoria, Dep. Caldas, a short distance northwest of Honda in the Bogotá collection, is buff tu buffy-white on the lower abdomen, while birds from the humid section of the valley to the north are fulvous underneath. The measurements of the pale population of the upper Magdalena valley suggest that it is slightly smaller than the richer colored form : 6 females (Carmen and Melgar, Dep. Tolima) wing 85 - 90, tail 70.5 - 74.4 compared to wing 88 - 94 and tail 70- -78 millimeters in birds from farther north (Chapman 1917 : 342).

The type of *N. radiatus* is buffy white below (Chapman 1917 : 342) and was probably taken in the drier portion of the upper Magdalena valley. For this reason the pale southern population should be considered the nominate form *N. radiatus radiatus*. The name "*Bucco fulvidus* Salvin & Godman, 1896" is available for the more intensively colored populations inhabiting the humid portions of the species range : *N. radiatus fulvidus*.

2. The Cauca and Patía valleys.

Lying between the Western and Central Cordilleras of Colombia, these valleys are separated from each other by the high plains of Popayán at 1750 meters elevation. The Rio Cauca flows north and joins the lower Rio Magdalena, while the Rio Patía flows southwest and cuts through the Western Cordillera in a narrow deep canyon emptying into the Pacific Ocean.

Cauca valley: only the northern very narrow portion west of Medellín and certain parts along the foot of the Western Cordillera are truly arid. The southern broad portion of the Cauca valley is more humid and fertile. However, due to intensive cultivation this part is today completely deforest-

ed. The few woodland species which entered this valley from the north (e.g. *Pipra erythrocephala, Formicarius analis)*, or from the west across the low Western Cordillera (e.g. *Manacus vitellinus)* have probably disappeared. The avifauna is closely related to that of the open Caribbean lowlands of northern Colombia, and is rich in endemic subspecies : in 30 species 13 forms are considered as distinct subspecies, while 17 are undifferentiated. The following species are not known from the Magdalena valley : *Leptotila plumbeiceps, Cypseloides lemosi, Ramphocelus flammigerus, Cyanocompsa cyanea* and *Ammodramus savannarum.* The smaller total number of species and the relatively high percentage of endemic forms of the Cauca valley compared to the Magdalena valley is probably due to its greater isolation (Chapman 1917).

Patia valley: a description of this isolated intermontane valley and a list of its avifauna have recently been given by Lehmann & Haffer (1967). From this data it is evident that the fauna is composed of widespread species of the open mountain slopes and of northern types of the Caribbean lowlands of Colombia. Practically all species which reached the Cauca valley have also advanced southward into the Patía valley. Some of the Patía populations are morphologically or in color somewhat different from those of the Cauca valley, but the differences are mostly too small to warrant a formal taxonomic recognition. A further group of species are inhabitants of the surrounding higher mountain slopes and range down to the valley floor at 600 meters above sea level *(Penelope montagnii, Cyanocorax yncas, Thamnophilus multistriatus, Basileuterus culicivorus).* The following subspecies inhabit both the upper Patía valley and the dry coastal lowlands of western Ecuador : *Myiopagis viridicata implacens* and *Saltator albicollis flavidicollis.* These forms as well as *Euphonia (concinna) saturata* and *Veniliornis callonotus* show a very restricted faunal exchange of the Arid Pacific fauna and the Colombia-Venezuelan nonforest fauna, which are otherwise completely isolated from each other (see below).

3. Smaller arid inter-Andean valleys.

Upper Dagua valley : The fauna of this arid pocket on the Pacific slope of the Western Cordillera was mainly derived from the Cauca valley across the low divide to the east (Chapman 1917 : 130). It is interesting to note that the endemic form *Polioptila plumbea daguae* is missing in the Cauca valley but reoccurs in the Patía valley.

The valley of the upper Rio Sucio above the town of Dabeiba is also located on the western slope of the Western Cordillera. It is not as arid as the upper Dagua valley, but its slopes are open and barren. Except for a few birds obtained by the collectors of the American Museum of Natural History (Chapman 1917) no representative collection has been made in this valley.

Chicamocha valley: This is a rather extensive dry pocket on the western slope of the Eastern Cordillera facing the humid middle Magdalena valley. It comprises the deeply incised valleys of the rivers Chicamocha, Suarez, Fonce and their smaller tributaries. The avifauna has been studied in detail by Borrero & Olivares (1955), see also Borrero & Hernandez (1958). The isolation of many bird populations in this dry pocket led to the development of several strongly differentiated species and subspecies, such as *Amazilia castaneiventris* (possibly representing the widespread *A. tzacatl*), *Thryothorus nicefori* (representing *T. rufalbus*), *Thamnophilus multistriatus oecotonophilus*, *Catharus aurantiirostris inornatus* and *Arremon schlegeli canidorsum*.

The Cúcuta valley is an arid pocket where the Eastern Cordillera of Colombia joins the Mérida Andes of Venezuela. It comprises the mountain valleys near the town of Cúcuta and around Urreña and San Cristobal. Characteristic species of the dry open country recorded from this area are *Sakesphorus melanonotus*, *Lepidopyga goudoti* and *Spinus cucullatus*. No species or subspecies appear to be restricted to this region today. The same is probably true for the valley of the Rio Chama, within the Mérida Andes of Venezuela.

3. THE ARID PACIFIC FAUNA.

This fauna inhabits the arid coastal lowlands of western Perú and Ecuador, south of the heavily forested Pacific lowlands of northwestern Ecuador and western Colombia. The fauna of the dry valley of the upper Rio Marañón is closely related to that of the Pacific lowlands (Chapman 1926, Dorst 1957) and is here included in the Arid Pacific fauna. Two main ecologic types are found in the arid Pacific lowlands: 1) The deserts of northern Chile and Perú, which appear to be of comparatively recent age and are inhabited by a fauna rather poor in well adapted desert forms (Koepcke 1961), and 2) the semi-deserts, steppes and dry deciduous woods of southwestern Ecuador and the upper Marañon valley with a richer bird life analysed in detail by Chapman (1926). From his data the following points are evident: the small total number of species and genera, the high percentage of endemic genera and species, some obvious relations to the Brazilian nonforest fauna and the very restricted relations to the nonforest faunas of northern South and Central America.

Among the endemic species and subspecies which show relations to the Brazilian fauna are the following : *Cyanocorax mystacalis*, *Synallaxis tithys*, *Sakesphorus bernardi*, *Melanopareia elegans*, *Columbigallina talpacoti buckleyi* (see M. Koepcke, 1962), *Furnarius leucopus cinnamomeus*, *Euscarthmus melorhyphus fulviceps*, *Fluvicola nengeta atripennis*, *Sicalis flaveola valida*, et cetera.

Species indicating some faunal exchange of the Arid Pacific fauna and the nonforest faunas to the north include the following: *Zenaida asiatica me-*

loda, Dives (dives) warscewiczi, Saltator albicollis flavidicollis, Myiopagis viridicata implacens and *Veniliornis callonotus*. The first two species are typically Middle American, while the remaining three forms are found both in the arid region of western Ecuador and in the Patía valley of southern Colombia (Lehmann & Haffer, 1966).

V. HISTORIC INTERPRETATION

The climatic history of South America during the Pleistocene and post-Pleistocene and in particular the repeated extension and contraction of the forests and nonforest vegetation, respectively, provide the basis for a historic interpretation of the zoogeographical data presented above. The assumption of the existence of extensive Tertiary forelands to explain present day distribution patterns in our area (Croizat 1958) seems largely unwarranted.

Colombian-Venezuelan nonforest fauna: it seems probable that the grassland savannas of the Guayanas and the isolated campos of the lower Amazon valley had a greater extension during several dry climatic periods of the past. They may have provided a more or less continuous pathway for Brazilian species to advance into the Venezuelan open plains of the Rio Orinoco. It seems likely that the isolated campos of the upper Rio Negro and Rio Branco region were also appreciably larger during some of the periods of drought. Strong-flying species may have crossed the forested Amazon valley from the Brazilian campos region (which reached farther north during these dry periods) to advance into the Llanos of eastern Colombia or vice versa. Sick (1959, 1963) has found a population of the northern *Aratinga pertinax* on an isolated campo in the area of the upper Rio Tapajós; this paroquet may have reached this region direcly from the Rio Branco area.

The repeated connection of the nonforest faunas to the north and south of the Amazon river through expanded (though possibly not continuous) campos and savannas along the lowlands of the Atlantic coast during periods of drought might explain the great number of species common to the Colombian-Venezuelan and the Brazilian nonforest faunas.

Only about half of those species which reached the Caribbean lowlands of northern Colombia have advanced northwestward into Central America. Probably most of the north Colombian lowlands, including the Urabá region and great parts of Panama, have been dry and unforested during dry climatic periods (Haffer 1967), providing a pathway for nonforest birds to advance into Central America and South America. However, it is also known that the sea-level rose by about 30 to 50 meters during the dry interglacials, thus flooding great parts of the north Colombian plains. The resulting large Caribbean embayments of the Maracaibo area, of the lower rivers Magdalena, Sinú

and Atrato must have hindered the faunal exchange appreciably (Haffer 1967, Fig. 3). The post-Pleistocene periods of drought were not accompanied by sea-level fluctuations. However, these dry periods may not have been arid enough to allow an unrestricted exchange of the savanna fauna through Panamá and the Urabá region. The comparatively restricted invasion of the South American *nonforest* fauna into Central America contrasts to that of the Amazonian *forest* fauna. The forest connection of northwestern Colombia and eastern Panamá was broad and uninterrupted during humid periods. Consequently a great number of Amazonian forest birds was able to advance into Central America (Haffer 1967). The above data may provide a historical explanation for the fact that "the number of recent South American elements is much smaller in the arid habitats of Central America than in the tropical rain forest" emphasized by Mayr (1964 : 285).

The faunas of the dry intermontane valleys of the Colombian Andes are closely related to that of the Caribbean lowlands despite their isolation by extensive forests today. The lack of endemic species in these valleys (except a few strongly differentiated forms in the Chicamocha area) suggests a frequent restoration of the connection between the dry areas during periods of drought when the forests were restricted to small "refuge areas". A repeated connection of the fauna of the Caribbean lowlands and that of the upper Magdalena valley was probably established when the humid forests, which cover the central portion of this valley today, largely disappeared during periods of drought (probably leaving only narrow piedmont forests along the base of the Central and Eastern Andes).

The isolation of the Cauca valley was more pronounced, as the northern entrance is a narrow canyon which was probably often blocked by forests of the wet Nechi Refuge even during dry climatic periods (Haffer, 1967). The relations between the faunas of the Cauca and the Patía valleys are very close. Connections were probably established during the dry interglacials when the separating high plains of Popayán presumably had a tropical climate.

During the humid climatic periods of the Pleistocene and post-Pleistocene the nonforest faunas retreated into small refuge areas, such as valleys in the rain shadows of the surrounding mountains, and portions of the Pacific slope of Central America. The north Colombian lowlands were probably much more extensively forest covered than today, providing a pathway for the Amazonian fauna to advance into the lowlands west of the Andes (Haffer 1967). However, dry refuge areas probably persisted farther away from the mountains, i.e. on the outer Guajira and Paraguaná Peninsulas, on the Orinoco plains, etc. at least during the upper Pleistocene and post-Pleistocene periods of drought.

Arid Pacific fauna: the extent of the area inhabited by this fauna probably fluctuated only little during the different climatic periods. During periods

of drought the arid region extended northward to the southern limit of the Chocó Refuge, while during humid periods this fauna retreated southward into northern Perú. H. W. Koepcke (1961 : 272) reported that the southern limit of mangroves was located near Bayóvar (latitude 6° S) during a sub-Recent humid climatic period, indicating that the humid tropical climate reached considerably farther south than today.

Zenaïda asiatica meloda and *Dives (dives) warscewiczi*, and possibly also *Burhinus superciliaris*, probably reached the area before the heavy forests developed along the Pacific coast of western Colombia at the beginning of the Pleistocene (Chapman 1926). A few species may have reached the arid Pacific coast from the Patía valley and vice versa (see above) sometime later during the Pleistocene or post-Pleistocene, when the Chocó forests had retreated northward.

The arid upper Marañón valley is separated from the west Brazilian and Bolivian savannas and campos by de Amazonian forest, which covers the lowlands to the foothills of the Andes (Fig. 1). A number of widely separated dry pockets are found today in deeply incised valleys in the eastern foothill zone of the mountain ranges. It seems probable that the Amazonian forest retreated somewhat to the north along de foot of the Andes during dry climatic periods. The dry pockets also probably enlarged individually and in number, thus possibly establishing a discontinuous connection of the Brazilian fauna with the Marañón and the Arid Pacific fauna. This interpretation is corroborated by the composition of the tropical avifauna of the lower Urubamba valley analysed by Chapman (1921). The deeply incised Urubamba valley ("U" in Fig. 1) is located half way between the Marañón valley and the present limit of the Bolivian savannas. Its lower part around Santa Ana is treeless and arid and the distinctive avifauna "...has evidently been derived through western Brazil..." (Chapman 1921 : 28). Out of a total of 66 species this author finds 38 to be of general distribution in the tropics. Of the remaining 28 no less than 19 are of Brazilian origin.

In summary, the Arid Pacific fauna is composed of highly endemic forms which may be of "pre-Andean" origin; they may have originated from populations which inhabited this area when the Andes still represented low, more or less unforested and possibly non-continuous ranges. Besides this predominating old element the fauna shows strong relations to the Brazilian fauna, probably through arid pockets along the eastern foothill zone of the Peruvian Andes. A few species may have reached the area from Central America, advancing south along the Pacific coast before dense forests developed in the Chocó area during the uplift of the Colombian Andes. The lack of any appreciable faunal exchange between the Arid Pacific fauna and the nonforest faunas to the north is additional proof for the long and independent history of the Chocó forests of western Colombia throughout the entire Pleistocene and post-Pleistocene (Haffer 1967).

Distributional gaps: In a number of species there are peculiar gaps in distribution. Rather small populations are separated by great distances from the main center of the range of the species. Today the intervening areas may be either suitable ecologically or unsuitable to these birds. A historic inter-pretation of these distribution patterns may be provided by the climatic history : Possibly the isolated populations reached their present distribution when suitable ecologic conditions permitted the expansion *. In some cases the isolated populations retained their restricted distribution later upon the return of suitable ecologic conditions in at least part of the intervening areas.

Gampsonyx swainsoni: Inhabits the greater part of nonforest South America to the Caribbean lowlands of northern Colombia and reoccurs in western Nicaragua.

Cranioleuca vulpina: Found in pastures and thickets near rivers and lagoons north to the Orinoco and Apure rivers of southern Venezuela. An isolated population of this species was recently discovered by Wetmore (1957) on Isla Coiba off de Pacific coast of Panamá.

Basileuterus flaveolus: The species is widespread in southern Brazil, Paraguay and Bolivia and reappears in coastal Venezuela.

Cyanocompsa cyanea: The species inhabits Brazil, Bolivia, Paraguay and Argentina. Isolated populations are found in northern Venezuela and in the Cauca-Patía valley of Colombia. The closely related *C. parellina* is found from Nicaragua to the north.

Oryzoborus crassirostris: South America to Brazil and Bolivia. An isolated population *(O. c. nuttingi)*, occurs on the Caribbean slopes of Nicaragua.

Spinus yarellii: Eastern Brazil and a restricted population in northern Venezuela.

Campylorhynchus griseus: Northern South America and a restricted population in Chiapas, Mexico.

<center>APPENDIX</center>

<center>COMPOSITION OF THE COLOMBIAN-VENEZUELAN NONFOREST FAUNA</center>

KEY : The names in *bold face type* indicate the endemic elements. The addition made to each species in parentheses means :

    in front of the comma : immigration (?, doubtful ; endemic species. Braz-from Brazil. C Am-from Central America).

    after the comma : emigration (dash-not found beyond the area of the Colombian-Venezuelan nonforest fauna. Pan-into Panamá. Mex-into Mexico, etc.).

    Arrows indicate undifferentiated populations.

* A similar explanation has been proposed by Eisenmann (1955: 7) and Duellman (1960, 1966: 706) for the history of isolated populations of Central American nonforest birds and reptiles, respectively.

I. *Species confined to the lowlands east of the Andes.*

Phacellodomus rufifrons (Braz, —), *Myiozetetes* **inornata** (?, —), *Empidonax euleri* (Braz, —), *Elaenia cristata* (Braz, —), **Quiscalus lugubris** (?, Braz and Lesser Antilles), **Gymnomystax mexicanus** (?, also found along rivers of the entire Amazon basin), *Spinus yarellii* (Braz, —), *Spinus* **cucullatus** (?, —), *Sicalis columbiana* (Braz, —), *Myospiza aurifrons* (Braz, —) *Basileuterus flaveolus* (Braz, —).

II. *Species advancing into the Caribbean lowlands of northern Colombia but not reaching the inter-Andean valleys.*

Crypturellus noctivagus (Braz, Mex : *C. cinnamomeus?*), *Gampsonyx swainsoni* (Braz, Nicaragua), *Scardafella squammata* (Braz, USA : *S. inca*), *Forpus passerinus* (Braz, —), *Aratinga acuticauda* (Braz, Mex : ? *A. canicularis*), *Furnarius leucopus* (Braz, —), *Sakesphorus canadensis* (Braz, —), *Myiarchus tyrannulus* (Braz, USA), *Inezia subflava* (Braz, —), *Tolmomyias flaviventris* (Braz, —), *Machetornis rixosus* (Braz, —), *Thryothorus* **rufalbus** (? C Am, Venezuela), *Nemosia pileata* (Braz, —), *Thraupis sayaca* (Braz, —). *Saltator coerulescens* (Braz, Mex), *Sicalis flaveola* * (Braz, —), *Sporophila plumbea* (Braz, —), *Sporophila lineola* (Braz, —), *Columba* **corensis** (?, —), *Aratinga* **pertinax** (?, Pan + Braz), *Leucippus* **fallax** (?, —), **Hypnelus ruficollis** + **bicinctus** (?, —), *Picumnus* **cinnamomeus** (?, —), *Poecilurus* **candei** (?, —), *Sakesphorus* **melanonotus** (?, —), *Inezia* **tenuirostris** (?, —), *Campylorhynchus* **nuchalis** (?, —), *Hylophilus* **aurantiifrons** (?, Pan), *Icterus* **nigrogularis** (?, —), *Icterus* **icterus** (Braz : *I. jamacaii*, —), *Pyrrhuloxia* **phoenicea** (C Am, —), *Saltator* **orenocensis** (?, —), *Arremon* **schlegeli** (Braz : *A. flavirostris*, —).

III. *Species reaching the Upper Magdalena valley.*

Caribbean lowlands	Upper Magdalena valley
Centurus **rubricapillus** (?, Costa Rica)......	→
Lepidopyga **goudoti** (?, —)...............	*L. g.* **goudoti**
Myrmeciza **longipes** (?, Pan).........	*M. l.* **boucardi**
Atalotriccus **pilaris** (?, Pan)	→
Campylorhynchus **griseus** (?, C Am and Braz)	*C. g.* **zimmeri**
Conirostrum **leucogenys** (?, Pan)...........	→
Burhinus bistriatus (C Am, Braz)......... ..	→
Amazona ochrocephala (Braz, Mex)........	-→
Speotyto cunicularia (Braz, USA)..........	*S. c.* **tolimae**
Chordeiles acutipennis (Braz, USA)	*C. a.* **crissalis**
Podager nacunda (Braz, —)	→
Nystalus radiatus (Chocó, Pan)	*N. r.* **radiatus**
Galbula ruficauda (Braz, —)	→
Thamnophilus doliatus (Braz, Mex)........	*T. d.* **albicans**
Formicivora grisea (Braz, Pan)............	→

* *S. flaveola* has been introduced in central Panamá (Eisenmann 1955).

Caribbean lowlands	Upper Magdalena valley
Manacus manacus (Braz, —)...............	*M. m.* **flaveolus**
Cnemotriccus fuscatus (Braz, —),...........	→
Idioptilon margaritaceiventer (Braz, —).....	*I. m.* **septentrionalis**
Euscarthmus melorhyphus (Braz, —).......	→
Hylophilus **flavipes** (♀, Costa Rica)........	→
Cyclarhis gujanensis (Braz, Mex)..........	→
Basileuterus delattrii (C Am, —)..........	→
Basileuterus rivularis (Braz, Honduras)	*B. r.* **motacilla**
Tiaris **bicolor** (♀, *Antilles*)................	*T. b.* **huilae**
Coryphospingus pileatus (Braz, —).........	*C. p.* **rostratus**
Arremon conirostris (C Am, Venez)........	*A. c.* **inexpectatus**

IV. *Species advancing both into the upper Magdalena and the Cauca-Patia valley*

Patía valley	Cauca valley	Caribbean lowlands	Upper Magdalena valley
	O. g. **caucae**	*Ortalis* **ruficauda+garrula** (♀, C Am)	*O.guttata* **columbiana**
	←	*Chrysolampis mosquitus* (Braz,—)	→
	←··	*Pachyramphus* **rufus** (♀, Braz and Pan)	→
	←	*Todirostrum sylvia* (Braz?, Mex)	→
	←–	*Ramphocelus* **dimidiatus** (♀, Pan)	*R. d.* **molochinus**
←	←	*Caracara plancus* (Braz, USA)	··→
←	←	*Tapera naevia* (Braz, Mex)	→
←	←	*Synallaxis albescens* (Braz, C. Rica)	→
←	←	*Pyrocephalus rubinus* (Braz, USA)	→
←	←	*Muscivora tyrannus* (Braz, Mex)	→
←·-	←	*Elaenia flavogaster* (Braz, Mex)	→
←	←	*Phaeomyias murina* (Braz, Pan)	→
←	←	*Sporophila* **intermedia** (♀, Braz)	*S. i.* **agustini**
←	←	*Sporophila minuta* (Braz, Mex)	→
←	←	*Myospiza humeralis* (Braz, —)	→
←	←	*Leistes militaris* (Braz, Pan)	→
←	*C. c.* **badius**	*Colinus* **cristatus** (♀, Guat.)	*C. c.* **leucotis**
←	*Z. a.* **caucae**	*Zenaida auriculata* (Braz, —)	→
←·-	*C. p.* **nana**	*Columbigallina* **passerina** (♀, USA)	*C. p.* **parvula**
←	*C. t.* **caucae**	*Columbigallina talpacoti* (Braz, Mex)	→
←	*L. v.* **decolor**	*Leptotila verreauxi* (Braz, Mex)	→
F. c. **pallescens** *	*F. c.* **caucae**	*Forpus* **conspicillatus** (♀, Pan)	→
M. v. implacens	*M. v.* **accola**	*Myiopagis viridicata* (Braz, Mex)	→
←	*C.a.***phaeopleurus**	*Catharus aurantiirostris* (C Am, Ven)	*C. a.* **insignis**
P. p. **daguae**		*Polioptila* **plumbea** (♀, Mex and Braz)	*P. p.* **anteocularis**
T. v. quaesita		*Thraupis virens* (Braz, Mex)	→
	E. saturata	*Euphonia* **trinitatis** (♀, C Am)	*E.* **concinna**
S. a. flavidicollis	←	*Saltator* **albicollis** (♀, Costa Rica)	→

* Described by Lehmann & Haffer (1967).

SUMMARY

The fauna of the unforested lowlands of Venezuela and Colombia is closely related to that of the nonforest regions of Brazil and eastern Bolivia. Endemic genera are very few and the number of endemic species is comparatively small. The dry intermontane valleys of the Colombian Andes were populated from the Caribbean lowlands to the north. Endemic forms of these valleys have reached the subspecies level and some are markedly different. The faunal exchange of the Colombian and Central American open-country fauna was rendered difficult even during the dry climatic periods of the Pleistocene due to partial flooding of the north Colombian plains.

The fauna of the arid Pacific coast of Ecuador and Perú has a great number of endemic genera and species. Some relations to the Brazilian nonforest fauna via the upper Marañón valley and dry pockets along the eastern base of the Peruvian Andes are evident in this fauna.

It is concluded that part of the Brazilian nonforest fauna surrounded the Amazonian forest in the east along the Atlantic coast and in the west along the base of the Peruvian Andes (to reach the upper Marañón valley) during dry climatic periods of the past, when the distribution of the forests was more restricted. A connection of the Colombian-Venezuelan nonforest fauna and the Arid Pacific fauna of Ecuador and Perú was prohibited by the Chocó forests (and the Chocó Refuge) along the Pacific coast of western Colombia. These forests formed a barrier to the nonforest fauna ever since they developed during the early-Pleistocene uplift of the Colombian Andes.

RESUMEN

Notas zoogeográficas sobre las avifaunas de las regiones no forestadas de Sudamérica noroccidental. — La avifauna de las planicies abiertas de Venezuela y Colombia muestra estrechas relaciones con la de las regiones abiertas de Brasil y Bolivia oriental. Solo hay dos géneros endémicos y el número de las especies endémicas es relativamente reducido. Los valles áridos de los Andes colombianos fueron poblados por la avifauna norteña de las planicies del Caribe. Formas endémicas de estos valles llegaron a nivel de subespecies, varias de ellas bien marcadas. El intercambio de las faunas de las regiones abiertas de Colombia y América Central fue obstaculizado por la inundación parcial de las planicies de Colombia durante los períodos secos del Pleistoceno.

La avifauna de la costa árida del Pacífico en Ecuador y Perú posee un gran número de géneros y especies endémicos. Son claras algunas conexiones con las aves del Brasil por vía del valle superior del río Marañón y algunos valles áridos a lo largo de la base de los Andes peruanos.

Se concluye que durante épocas secas del pasado, parte de la avifauna de las regiones abiertas del Brasil extendió su área de distribución a lo largo de la costa del Atlántico

para llegar a las planicies de Venezuela y Colombia, y además, siguiendo la base de los Andes del Perú hasta llegar al valle del río Marañón y a la costa del Pacífico. Sin embargo, las selvas de Colombia occidental, en la región del Chocó, impidieron el intercambio de las avifaunas de las planicies abiertas de Colombia septentrional y de las costas ecuatorianas y peruanas.

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