

A ZOOGEOGRAPHIC ANALYSIS
OF THE SOUTH AMERICAN
CHACO AVIFAUNA

LESTER L. SHORT

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 154 : ARTICLE 3 NEW YORK : 1975

A ZOOGEOGRAPHIC ANALYSIS
OF THE SOUTH AMERICAN
CHACO AVIFAUNA

LESTER L. SHORT

*Curator, Department of Ornithology
The American Museum of Natural History
Adjunct Professor, City University of New York*

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 154 : ARTICLE 3 NEW YORK : 1975

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Volume 154, article 3, pages 163-352, figures 1-82, table 1

Issued January 3, 1975

Price \$9.60 a copy

ISSN 0003-0090

Copyright © The American Museum of Natural History 1975

CONTENTS

Abstract	167
Introduction	167
Methods and Materials	168
Acknowledgments	169
Description of the Chaco	169
Systematic Accounts of Chaco Birds	179
Family Rheidae	186
Family Tinamidae	186
Family Podicipedidae	192
Family Phalacrocoracidae	193
Family Anhingidae	193
Family Ardeidae	193
Family Ciconiidae	195
Family Threskiornithidae	196
Family Anhimidae	197
Family Anatidae	198
Family Cathartidae	200
Family Accipitridae	201
Family Falconidae	207
Family Cracidae	210
Family Aramidae	211
Family Rallidae	212
Family Cariamidae	216
Family Jacanidae	217
Family Rostratulidae	217
Family Charadriidae	217
Family Scolopacidae	218
Family Recurvirostridae	219
Family Laridae	219
Family Rynchopidae	220
Family Columbidae	220
Family Psittacidae	224
Family Cuculidae	230
Family Tytonidae	232
Family Strigidae	232
Family Nyctibiidae	236
Family Caprimulgidae	236
Family Apodidae	238
Family Trochilidae	239
Family Trogonidae	241
Family Alcedinidae	242
Family Momotidae	243
Family Bucconidae	243
Family Ramphastidae	244
Family Picidae	245
Family Dendrocolaptidae	253

Family Furnariidae	255
Family Formicariidae	261
Family Rhinocryptidae	264
Family Cotingidae	265
Family Tyrannidae	268
Family Phytotomidae	285
Family Hirundinidae	285
Family Corvidae	288
Family Troglodytidae	289
Family Mimidae	290
Family Turdidae	291
Family Sylviidae	292
Family Motacillidae	293
Family Vireonidae	293
Family Icteridae	294
Family Parulidae	299
Family Thraupidae	302
Family Emberizidae	307
Family Carduelidae	323
The Distribution of Chaco Birds	325
The Occurrence of Chaco Birds Outside of South America	325
Endemicity in the Chaco	329
Avian Distribution in the Chaco and Surrounding Regions	329
Major Disjunctions in Range Among Bird Species Occurring in the Chaco	335
Conspecific Range Disjunction	335
Disjunctions among Allospecies of Superspecies	338
Discussion	340
Zones of Avian Interaction and Narrow Range Disjunctions	342
Discussion	345
Zones of Primary Integradation Amont Chaco Birds	347
Origins of the Chaco Avifauna	348
Literature Cited	349

ABSTRACT¹

The South American chaco is centrally situated on the border of the tropics and is xeric-adapted woodland with some open areas, wet places, and savanna. Driest in the center and wettest in the eastern pantanal savanna, the chaco experiences occasional frost throughout. About 409 avian species, including 22 that barely reach its borders, are resident or breed in the chaco. These number 218 nonpasserine birds, 100 suboscine passerines, including 52 tyrant flycatchers, 20 oscine passerines of Old World groups, and 71 New World nine-primaried oscines. Each species is treated taxonomically (based on a systematic reappraisal of each taxon), ecologically, and distributionally. There seem to be more superspecies in the chaco and in the tropics generally than in temperate North America. Most chaco species (252) are endemic in South America, but 28 percent reach Middle America, 12 percent attain North America, and 3 percent reach the Old World. A transatlantic distributional history is possible for as many as one-seventh the number of chaco species reaching North America. Only one species (*Eudromia formosa*) is endemic to the chaco; 11 others mainly occupy that area; five subspecies are endemic. Such low endemism reflects the central location and accessibility of the chaco, and probably rather drastic historical changes in its extent and location. Major range disjunctions in chaco species and superspecies frequently involve northern South America, with Amazonia the apparent barrier. Isolates in the Andes and in the coastal Peru region are fewer, but well differ-

entiated. The caatinga is another area of differentiation. Zones of avian interaction (70) and narrow range disjunctions (28) involving chaco birds show isolates and former isolates mainly in southeastern Brazil, in the campo-caatinga region, and in the Andes, indicating that barriers (e.g., grassland, water) exist or formerly existed between the paired forms. Significantly more nine-primaried oscines and fewer nonpasserine birds show interactions and narrow disjunctions compared with proportions of these species in the chaco avifauna. This perhaps reflects greater speciation and radiation in the nine-primaried oscines, a group still relatively new to southern South America. Primary intergradation in the 276 polytypic chaco species indicates the coincidence of racial borders with major environmental features such as the Amazon and Paraguay rivers, and with certain regions (campo cerrado, Andean base). Major size differences among races of 81 chaco species generally agree (69 cases) with Bergmann's Ecogeographic Rule, larger forms occurring south of smaller races. The chaco avifauna largely is derived from elsewhere, particularly from other xeric regions, savanna formations and edges or ecotones involving forested regions. The chaco nevertheless has been important in furthering range extension and the ultimate isolation of some xeric-adapted birds and species favoring edges and ecotones. There is a need for further in-depth taxonomic-zoogeographic investigations of particular Neotropical avian groups and regional South American zoogeographic analyses.

INTRODUCTION

I have selected for a zoogeographic analysis the South American chaco avifauna for reasons both scientific and emotional. Scientific reasons include the almost central location of the chaco in South America, its proximity to temperate and tropical areas, and avifaunally, its low endemism. Zoogeographers usually are interested in areas of high endemism, but my purpose here is

to attempt derivation and relations of what appears to be a mixed and perhaps recently derived avifauna. The emotional reasons are my fascination for xeric regions, in which I have been fortunate to study birds on three continents, and my desire to understand the history and evolution of faunas inhabiting such regions.

The chaco (fig. 1) is a flat, low plain covered with a relatively uniform arboreal growth. No physical barriers of significance operate to restrict entry into or departure from the chaco by birds. The only apparent physical barrier, the

¹ I dedicate this report to outstanding evolutionary biologist Ernst Mayr on the occasion of his seventieth birthday.

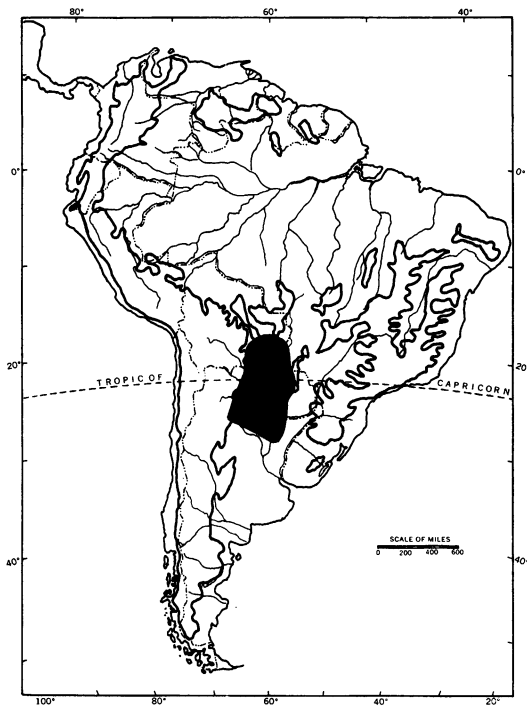


FIG. 1. Location of chaco in South America. A dark line approximately borders upland areas above 1200 feet in elevation.

rather broad Paraguay-Parana river system, serves as an eastern limit for some birds, but many species cross the river and enter Mato Grosso, eastern Paraguay, Corrientes, and Entre Ríos, and, indeed, chaco woodlands occur on the east side of these rivers in Mato Grosso, Corrientes, and Entre Ríos. There are direct connections of the chaco with Amazonian forest in the northwest, campo cerrado in the northeast, southeastern Brazilian subtropical moist forest in the east, pampas in the southeast and south, and lower Andean steppe, "monte," and dry subtropical forest in the west. Aspects of the ecology and avifauna, especially in Paraguay and Formosa, Argentina, were treated by Laubmann (1930, 1939) and by Steinbacher (1962).

The chaco lies south of the main ranges of most Amazonian species, and the number of breeding species thus is a moderate 409, which in the current state of our knowledge of the taxonomy of South American birds can be analyzed

more readily than richer avifaunas to the north. At the same time, the chaco is on the fringe of the tropics (the Tropic of Capricorn almost exactly bisects the chaco) and is influenced by them; hence more species occur than in the temperate areas farther south. I hope that a diligent taxonomic appraisal of this limited number of species, and the zoogeographic analysis of these chaco species will contribute generally to South American avian taxonomy and faunistics.

METHODS AND MATERIALS

I ascertained, by consulting the pertinent literature, the distribution of avian species known to occur or suspected of occurring in the chaco. Maps were prepared indicating the ranges of all such species. Meyer de Schauensee's (1966, 1970) treatises provided data for the initial survey, but many other publications were consulted, including the works of Naumburg (1930), Laubmann (1930, 1939, 1940), Olog (1959, 1963, 1968), Steinbacher (1962, 1968), and the many revisionary works of John T. Zimmer, as well as revisions of major groups (e.g., Goodwin, 1967; Brown and Amadon, 1968; Vaurie, 1968; and others). The distributional information was tempered by my own field experience (in Salta, Formosa, eastern Chaco Province, northern Santa Fe, Corrientes, Tucumán, and Santiago del Estero) in the chaco during September and October, 1967, and September and October, 1968. I also consulted collections at various North American and European museums, and especially the fine Kaempfer collection (some of which has not been reported in the literature) in the American Museum of Natural History. My taxonomic approach at the generic level has been stated elsewhere (Short, 1967, pp. 11-12), as have my concepts of species and secondary contact phenomena (Short, 1965, 1969a, 1969b). The particular approach involving consideration of relationships on a broad geographical basis and utilization of the superspecies concept follows that of Mayr and Short (1970).

Systematists of South American birds know that much still remains to be learned. The relationships expressed herein are in some cases tentative, but in such instances they provide models for consideration by future taxonomists and especially field workers. Because of this I have

gone into detail about my reasons for the systematic treatment I employed. In any event, I suspect that the relationships I state below will not be modified so substantially as to affect the conclusions resulting from the analysis.

The distributional and taxonomic data were employed in the analysis of geography of the chaco avifauna. An attempt is made to establish some ecological correlates of distributional patterns and to derive the chaco avifauna from its areas of origin. Standard zoogeographical procedures were used throughout the study, which, like all such investigations, depends for its success upon its systematic and distributional foundation.

ACKNOWLEDGMENTS

I thank my colleagues at the American Muse-

um of Natural History, especially Drs. Dean Amadon and Charles Vaurie, for assistance. Mrs. Sheila C. Short assembled distributional data and prepared preliminary maps of the ranges of all species considered in this report. Messrs. Richard S. Crossin and John J. Morony, Jr., assisted with the field studies. The National Science Foundation provided funds (NSF-GB-5891) in support of many aspects of this study and of taxonomic investigations the results of which are incorporated in the present report. Matters of taxonomy were discussed with many specialists, too numerous to name individually, but I would be remiss not to mention especially Drs. Dean Amadon, Walter J. Bock, Wesley E. Lanyon, Kenneth C. Parkes, Charles Vaurie, and François Vuilleumier. The taxonomic views expressed herein, however, are my own.

DESCRIPTION OF THE CHACO

PHYSICAL FEATURES OF THE CHACO

The chaco is a vast, low plain, virtually unbroken by hills, situated in the rain shadow of the Andes Mountains and far from the Atlantic Ocean. It stretches from Santa Cruz, Bolivia, south to northern Córdoba, Argentina, and from the Paraguay River west to the base of the Andes. Measuring roughly 1500 km. from north to south, and 700 km. from east to west, the chaco covers an area of about 1,000,000 sq. km. Included within the chaco are: about the southern third of Santa Cruz, Bolivia (100,000 sq. km., Hueck, 1966); all of western Paraguay (possibly the southwestern corner of eastern Paraguay, south of Asunción, should be included); easternmost Chuquisaca, and Tarija, Bolivia (east of Villa Montes); southwestern Mato Grosso near the Paraguay River (about Porto Esperanza south to the Paraguayan border, 7000 sq. km., Hueck, 1966); and north-central Argentina including all of Formosa, Chaco, Santiago del Estero, the northeastern corner of Salta, easternmost Tucumán, the northern third of Santa Fe, the northwestern corner of Entre Ríos, and the western third of Corrientes (Short, 1971b). Much of the eastern and southern portion of the chaco is below 100 m. elevation. There is a gradual rise to

the northwest, with elevations of 450 m. attained in Salta and other areas at the base of the Andes. The soil of the region consists of sandy loess, loess loam, and alluvium on a base of Tertiary clay, marl, gypsum, and salt (Hueck, 1966). There is little or no humus in most of the chaco. Low areas with poor exterior drainage in Santiago del Estero, northern Paraguay, and Bolivia have extensive salt pans, the salt in places excluding all vegetation.

There are few major rivers, and running water is scarce. The large south-flowing Paraguay-Parana river, flowing from headwaters in Mato Grosso and the hills of central Santa Cruz, affects the climate, vegetation, and fauna of the entire eastern chaco, as is discussed below. Otherwise, the few major rivers (Pilcomayo, Bermejo, Salada) flow from the Andes southeast across the chaco to meet the Paraguay-Parana, bearing much water in the wet season, but diminishing greatly or even disappearing in the dry season. As Hueck (1966, p. 218) has noted, these chaco river courses are distinctly different from the surrounding country, affecting nearby areas very markedly through flooding, but not having a significant effect beyond those areas. Except along these water courses, and in the eastern and northern edges of the chaco, the ground water level

usually is at such great depth as to be beyond the reach of root systems of plants.

Rainfall varies from a low 500 mm. or less in the center of the chaco (Santiago del Estero, western Formosa), increasing both to the west and the east to as much as 1000 or even 1200 mm. along the Paraguay-Parana river, and to 800 mm. at the base of the Andes in the west (Gorham, 1973). As much as 80 percent of the rainfall occurs in the summer from November to April. Rain in the dry season may be less than 40 mm. for one or more months (Eidt, 1968). Much of the precipitation comes in cloudbursts and heavy rains, which cause erosion and result in rapid runoff and loss of water. Hail and thunderstorms are not uncommon, and sand storms sometimes occur. In the arid center of the southern chaco there is a depression of the land, with some areas below sea level. Within this region evaporation exceeds precipitation, the dry season is prolonged, and periods of up to eight or 10 weeks may pass without significant rain.

Yearly mean temperatures in the chaco are from 18° to 25° C. Santa Cruz, Bolivia, at 25° C., and western Paraguay at 23° to 24° C. are warmer than areas to the south. South of Paraguay temperatures drop markedly with means from 20.6° C. in Santiago del Estero to 17° C. in Córdoba, just south of the chaco. Monthly mean temperature ranges from within 6° C. in the north to 14° in the south. Maximum temperatures occur in Santiago del Estero and eastern Tucumán, and may reach 48° C. (the south-central chaco has experienced the greatest temperatures known in South America). Minimum temperatures below freezing occur almost everywhere, although not yearly in the north. Even in southern Santa Cruz minimum temperatures of -5° C. occur almost yearly (Hueck, 1966). Temperatures rise rapidly during the day, however, and extended periods of freezing are almost unknown. Extremes of temperature are less in proximity to the Paraguay-Parana river due to fog, and the region about the Paraguay River in northern Paraguay and Mato Grosso is the only part of the chaco in which freezing temperatures are virtually unknown. Snow is rare in the chaco, as might be expected from the infrequent occurrence of subfreezing temperatures, the rapid rise in temperature following freezing, and infre-

quency of precipitation in any form in the winter dry season.

Most of the chaco climate must be considered temperate rather than tropical. Temperatures averaging 18° C. or more every month of the year occur only in the Mato Grosso and northernmost Paraguayan chaco near the Paraguay River (Eidt, 1968), hence only this area of the chaco can be designated as tropical. Easternmost Santa Cruz and northern Paraguay, the vicinity of the Paraguay River in central and southern Paraguay, and eastern Formosa and northeastern Chaco Province may be considered subtropical. Freezing temperatures are rare within this zone. The remainder of the chaco from southern Santa Cruz south to northern Córdoba, and from the east-central part of the Paraguayan chaco, east-central Formosa, and northwestern Entre Ríos westward to Tarija and Tucumán, is within the Temperate Zone (Eidt, 1968).

PLEISTOCENE AND POST-PLEISTOCENE HISTORY

Immense changes occurred in South America at the end of the Tertiary as uplift of the future Andes Mountains commenced. Today there is no clear indication of what the chaco region was like (see Putzer, 1962) prior to the orogeny responsible for the Andean uplift, which took place mainly in the late Pliocene and early Pleistocene. The low avifaunal endemism of the chaco (even botanically endemism is mainly at the species level, Hueck, 1966) suggests that the present chaco is a recent development with a floral and faunal composition derived from several external sources.

Little concerning the history of the chaco is known, and much remains to be learned about the Pleistocene (Vuilleumier, 1971) of South America. There is little or no data on the extent of up- or down-warping of the chaco in the late Pleistocene. Viewing the low, flat topography of the chaco and its location in South America, one can assume major changes simply due to shifts in sea level between full glacio-pluvial periods and interglacial periods. A rise of 50 m. in sea level, which seems plausible for interglacials (Haffer, 1969), may have inundated the southern and eastern parts of the

chaco. At the same time swamps, "esteros" and "bañados" such as the vast Bañados del Izoog at the northwestern chaco border in southwestern Santa Cruz, the Esteros del Iberá at the eastern chaco border in Corrientes, and the pantanal along the Parana-Paraguay river in Argentina, Paraguay, and Mato Grosso may have expanded greatly. On the other hand, lowered sea level of 100 to 125 m. in the most recent (Würm-Wisconsin) glacial period allowed connection of southern South America with the Falkland Islands, resulting in a greatly expanded continental area southeast of the chaco (Auer, 1970). At that time what is the present chaco region was farther from the presumably more humid coast. There is evidence for the occurrence of semiarid (steppe?) conditions in much of the chaco (Groot and Groot, 1966), probably during glacial times.

In any case there is substantial agreement (see e.g., Lüders, 1961; Groot and Groot, 1966; Haffer, 1969; and Auer, 1970) that dry and moist conditions alternated during the Pleistocene. These phases were not correlated moist with glacial and dry with interglacial periods, for, according to Groot and Groot (1966) the semiarid steppe region east of the Andes was particularly large during glacial periods, when the sea level was low. Bigarella and Ab' Sáber (1964), Bigarella, Mousinho, and Da Silva (1965), and Bakker (1968) indicated that Atlantic coastal Guiana and southeastern Brazil were arid during glacial periods. Postglacial fluctuations from arid to humid to semiarid have been suggested for the chaco by Lüders (1961).

According to Auer (1970), the connection of the Argentine continental shelf with the Falkland Islands during the Würm-Wisconsin caused the obstruction of the Cape Horn Current, permitting the flow of warm water southward, and mangroves grew on the coast of Patagonia. The postglacial eustatic rise in sea level cut the connection with the Falklands, and the Cape Horn Current again affected eastern South America. Auer presents a convincing picture of steppe-forest alternation in conjunction with arid-humid cycles. At some time in the Pleistocene, perhaps during interglacials, forests extended south over the pampas perhaps to Patagonia. Evidence for the former extension of forests to the south in-

cludes the occurrence of isolated patches of *Araucaria braziliensis* as relicts in parts of Uruguay (Tower, 1918). Arid conditions along the Brazilian coast from Bahía to Rio Grande do Sul, noted above, may have enabled a chaco-caatinga connection as recently as the Würm-Wisconsin glacial period.

In summary, the chaco was arid during dry periods of the Pleistocene, with an extension of scrub vegetation and even steppe through at least the western chaco. In more humid times vegetation was lush in the western chaco than it is at present, particularly along water courses. Great swamps and extensive palm savannas, fringed with forest probably characterized the eastern chaco during wet periods. Embayment of the lower Parana River during interglacials may have occurred in conjunction with high ground water and extensive swamps from Mato Grosso to the delta of the Parana. Full glacial periods probably were characterized by very dry conditions in at least the western chaco. Correlation of wet-dry cycles with glacial-interglacial periods is uncertain, as Haffer (1969) noted. Major xeric-mesic fluctuations have occurred postglacially in the chaco, as well as to the south (Pampas, Auer, 1970) and to the north (Amazonia, Haffer, 1969, 1970a).

AVIAN HABITATS IN THE CHACO

The vegetation of the chaco has been characterized by Hueck (1966) and much of the discussion that follows is based on his data. In relation to bird habitats Laubmann (1930) has discussed the chaco, and others, especially Wetmore (1926), have described some avian habitats in that region. It should be emphasized that the characteristics of the form of vegetation are important to birds, but very often nuances of plant species variations appearing important to botanists are of little significance in avian distribution. Those chaco habitats believed to be of importance to birds are summarized as follows, and then discussed individually:

- A. Water habitats
- B. Treeless terrestrial habitats
 - a. Salt pans
 - b. Sand dunes

- c. Grasslands
- d. Cultivated land and pasture
- C. Woodlands
 - a. Dry (Algarrobo-Quebracho-Palo Santo) woodlands
 - b. Tala-Mistol woodlands
 - c. Pantanal
 - d. Gallery forest and shrub woodlands
- A. Water habitats: Birds dependent on water for foraging and breeding are uncommon in much of the chaco. Permanent surface water occurs mainly in the lower reaches of the major chaco rivers mentioned above, in wet areas in the pantanal, along the Paraguay-Parana river, and in the few flooded swamps that occupy sizable portions of the Paraguay River basin in Mato Grosso-Santa Cruz, and in southwestern Santa Cruz. No major lakes are found in the chaco (the large Mar Chiquita is just south of the chaco in Córdoba). Esteros and swamps of large size (fig. 2) are uncommon, and are usually along bypassed segments of old river courses. Few water birds are found away from the major rivers.

B-a. Salt pans: Very salty areas bordering major salt pans, such as that of Salinas Grandes in Santiago del Estero, do not support woodland, but have a cover of low halophytic plants, especially *Suaeda divaricata*, species of *Allenrolfia*,

and *Heterostachys ritteriana* (Hueck, 1966). Of these *Suaeda* attains the size of a tree (to 6 m.). Nothing is known of the birds frequenting this vegetation. The actual salt pans are virtually devoid of vegetation.

B-b. Sand dunes: Shifting sand dunes occur at a few places in the chaco, especially in northern Paraguay and Santa Cruz.

B-c. Grasslands: Natural grasslands are uncommon in the chaco, except in the pampas-chaco ecotone at the southern and eastern border of the chaco. Hueck (1966) believed that treeless areas of the chaco originally included mainly the vicinity of salt pans and flooded swamps. There is no evidence for the occurrence of extensive grasslands within the chaco proper. Birds of these habitats, such as *Colaptes campestris* and pipits (*Anthus* sp.), were either confined to the pantanal originally, or have invaded the region since initiation of clearing and cultivating by man.

B-d. Cultivated land and pasture: Large areas of the chaco have been converted into cultivated land and pasture through cutting, clearing, and burning. This has "opened" up much of the southern and southeastern chaco and portions of the remainder. Species of birds favoring woodland edges, villages and the vicinity of habitations, cultivated fields, and open country gener-



FIG. 2. Large estero (marshy lake) in southern chaco, 25 km. W of Villa Ana, northern Santa Fe, Argentina. October 3, 1968.

ally have benefited. Unfortunately we have too little information from earlier periods to enable us to state that any bird has newly entered the chaco because of human activities (of course, introduced species such as *Passer domesticus* are exceptions).

C-a. Dry (Algarrobo-Quebracho-Palo Santo) woodlands: This is the "type" habitat of the chaco, responsible for its distinctness and characterizing a great part of it. Variation exists among different types of dry woodland, but there are no avifaunal data upon which to base a separation of these types. Far more important for birds than these variations are the effects of man in modifying and destroying the dry chaco woodlands. Selective cutting of quebracho and other valuable trees, firewood-gathering, and grazing by cattle have changed vast areas—perhaps most—of the chaco, particularly in Argentina. All of these acts have drastically changed the woodlands, resulting in the presence of more cacti and other hardy species, wind erosion and reduction of top soil, and a generally more xeric woodland. Vast areas additionally are being destroyed altogether; as an example, Hueck (1966, p. 244) cited the burning of 150,000 tons of quebracho wood yearly by the seasonally operated sugar refineries in Tucumán (railroads, other industries, and the local inhabitants make further inroads there and in much of the Argentine chaco). In contrast, variation among the types of dry woodland is variation on a common theme.

Algarrobo woodland occurs primarily in the driest parts of the chaco, and especially where salt is present at the soil surface. Dominant elements of this woodland often form second growth in disturbed situations as around villages. Most of the trees and bushes in this woodland occur in other dry woodlands as well. Dominant species are the mesquites or "algarrobos" *Prosopis alba* and *P. nigra*, which reach heights of 12 m. This vegetation gives way to halophytic plants (mentioned above) in the immediate vicinity of salt pans. Firewood-cutting and other use of these woodlands has increased the prevalence of cacti, notably *Cereus coryne*, *C. validus*, and *Opuntia quimile*, and ground bromeliads (*Bromelia*, *Dyckia*). This type of woodland occurs sporadically throughout the chaco, except in Mato Grosso (Hueck, 1966).

On less salty soil Algarrobo woodland is replaced by Quebracho woodland, which forms the main woodland of the central chaco. In dense stands a slight amount of humus may form. Among the dominants are the economically important *Aspidosperma quebracho-blanco* and *Schinopsis quebracho-colorado*. Cutting for these trees (for tannin, lumber, firewood) has devastated much of the woodland, such that extensive uncut stands exist only in northern Paraguay and Bolivia. This lumbering tends to favor such species as algarrobo. Other trees are *Zizyphus mistol*, *Geoffroea decorticans*, *Bulnesia sarmientoi*, *Chorizia insignis*, the palm *Trithrinax campestris* (a dominant in some areas), and others including species of *Cercidium*, a xeric group whose species reach the Sonoran Desert of North America. Many arborescent cacti occur in this woodland (fig. 3), including several species of *Cereus* and of *Opuntia*, and also *Cleistocactus*, *Trichocereus*, and others. Shrubs are mainly xeromorphic, including species of *Maytenus*, *Mimosa*, *Condalia*, *Ephedra*, and others. Species of *Tillandsia* and *Usnea* are present as epiphytes, several mistletoes are common, and the ground is literally covered in many places with armed *Bromelia hieronymi*, which makes walking painful or impossible. To the east, more moist conditions favor occurrence as a dominant of a different "quebracho," *Schinopsis balanse*, which attains a height of 20 m. and is not found in the central or western chaco. The eastern chaco dry woodland often is restricted to higher ground in the pantanal region along the Paraguay-Parana river, and east of that river system (in Corrientes) it is mixed with subtropical moist forest elements derived from southeastern Brazil and Misiones.

Palo Santo-Quebracho woodland occurs in the northern part of the Argentine chaco, Paraguay, and Bolivia. The economically important Palo Santo (*Bulnesia sarmientoi*) is scattered in the Quebracho woodland, and rarely occurs in pure stands. Quebracho woodland extends to the base of the Andes Mountains. At the edge of the mountains it mixes with the deciduous subtropical dry forest that extends south along the Andes from Bolivia. The dry nature of the foothills of the Andes results in mountain-Quebracho woodland extending to their tops (elevations to 1300 m.). The low precipitation prevents formation of

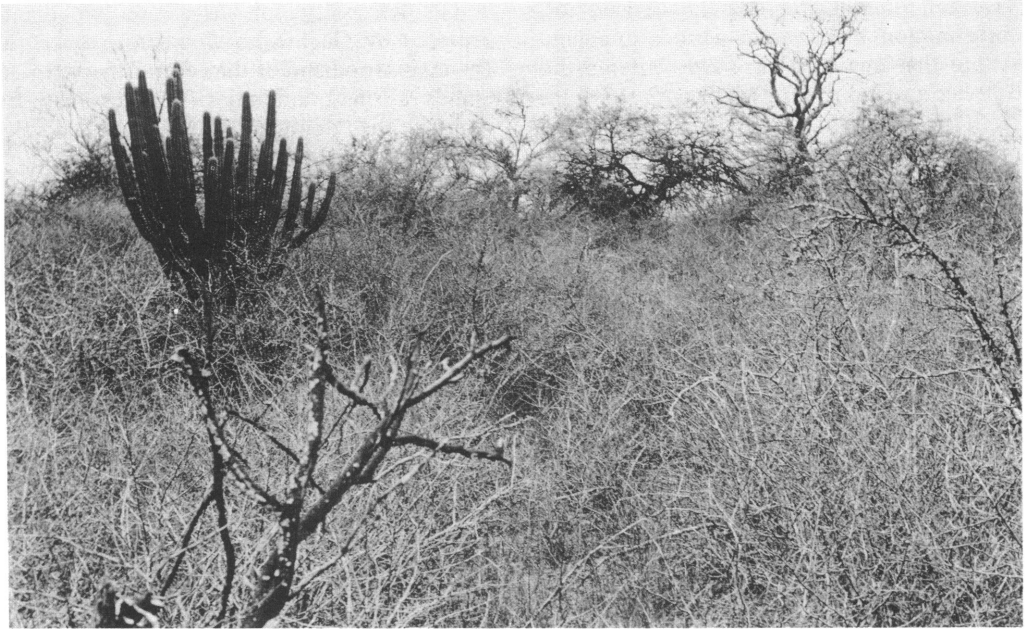


FIG. 3. Thorn forest aspect of (largely algarrobo, see text) chaco woods, 50 km. E of Pozo del Tigre, Formosa, Argentina. September 14, 1968.

more moist forest. This mountain-Quebracho woodland is an extension of the chaco, featuring a species confined to this area, *Schinopsis haenkeana*, and especially large bottle trees (*Chorisia insignis*).

C-b. Tala-Mistol woodland: This is the woodland type of the western chaco where precipitation is between 600 and 800 mm. It forms the western transition (fig. 4) to more mesophytic, nonchaco woodlands. Isolated sites in the central chaco with ground water near the surface also contain this woodland type. Dominant elements are the Tala (*Celtis pubescens*) and the Mistol (*Zizyphus mistol*); the latter occurs sporadically throughout the chaco, even into western Corrientes. Basically, this formation includes larger leaved, more mesophytic species of plants, and cacti and other xeromorphic species are much less prominent than in the central chaco. Other important elements include *Scutia buxifolia* and *Pisonia zapallo*. This woodland grades into more mesophytic, taller (to 30 m.) forest characterized by the presence of *Tipuana tipu*, and *Enterolobium contortisiliquum*, and in the north *Calyphyllum multiflorum*. The lowland portion of

this transition forest at the edge of the chaco is almost totally gone; this is the region favoring cultivation of various crops, including sugar cane, and the forest has been removed except for small isolated patches. Certain chaco species such as *Cupania vernalis*, *Cedrela lilloi*, *Tabebuia avelanadae* and others extend into the subtropical forest of the mountain slopes and there attain heights greater than achieved anywhere in the chaco.

C-c. Pantanal: Although Hueck (1966) has employed this term only in reference to the "Grande Pantanal" of Mato Grosso, an area of swamps, small lakes, and sluggish streams in which trees are restricted to higher ground, I favor broader usage to include the palm savannas (fig. 5) bordering the gallery forests along the Paraguay-Parana river from Mato Grosso to northern Chaco and Corrientes. These palm savannas (mainly called *Copernicia* woodland by Hueck, *op. cit.*) are situated on soil in which ground water is almost at the surface. Much of the pantanal is flooded for part of the year in the rainy season. True pantanal is low wet grassland with palm trees in groves or sprinkled throughout



FIG. 4. Western chaco (Tala-Mistol woodland) and subtropical dry forest form ecotone in north-eastern Salta, as shown here. North of Senda Hachada, Salta, Argentina. September 13, 1968.



FIG. 5. Pantanal of eastern Formosa, near Formosa (city), Argentina. Open wet to dry (seasonally) grassland with interspersed palms (*Copernicia australis*) and isolated chaco forest groves. September 16, 1968.

the grasslands or around the borders of wetter areas. The palms are predominantly *Copernicia australis*, and also *Trithrinax campestris*, and, east of the Paraguay-Parana river, *Arecastrum romanzoffianum* and *Acrocomia totai*. The species of *Trithrinax* and *Copernicia* are typical of the chaco and occur in other chaco woodlands (*Copernicia australis* is closely related to *C. cerifera*, the wax palm of the Brazilian campos). *Arecastrum* and *Acrocomia* are found in subtropical forests of eastern Paraguay and southern Brazil. *Copernicia australis* far outnumbers other palms, and often occurs in pure stands. Drier (higher) areas within (fig. 6) the pantanal contain woodlands typical of the eastern chaco, or, as in Corrientes, mixed with elements derived from the wet subtropical forest of Misiones and Brazil, and from gallery forests, as well as with palms from the adjacent pantanal. In eastern Corrientes and eastern Paraguay more xeromorphic elements of the chaco woodland are lacking. Drier woodlands persist despite the ground water and great precipitation, because of the long dry season. *Copernicia australis* forms occasional groves within the chaco wherever the water table is near the surface (e.g., old river beds), and extensive

“palmares” near the base of the Andes about Villa Montes and Yacuiba, Bolivia (Hueck, 1966).

The pantanal provides a habitat in the chaco for certain water birds and open country (campo, pampas, savanna) species. Chaco woodland species occur in its dry woodland “islands.”

C-d. Gallery forest and shrub woodland: Gallery forests extend along the Paraguay-Parana river, the various channels of the lower (fig. 7) Río Pilcomayo, the lower Río Bermejo, and for some distance along the last two rivers and other minor rivers where they emanate from the Andes and enter the western chaco. The soil is level and ground water is within reach of the root systems of trees. Gallery forests are lacking along parts of the Paraguay River, but are present elsewhere (fig. 8), and are especially well developed along the Upper Parana River in Corrientes. Indeed the Upper Parana River carries with it subtropical moist forest elements from Misiones. These drop out gradually to the west, and more rapidly to the south of the junction with the Paraguay River. This somewhat impoverished subtropical forest element is enriched by broadly distributed South American species like *Salix humboldtiana*



FIG. 6. Edge of isolated, partly cut-over quebracho woods in pantanal near Paraguay River, 60 km. SE of Formosa (city), Argentina. September 28, 1968.



FIG. 7. Edge of gallery forest, 14 km. NW of Espinillo, just S of Pilcomayo River, northern Formosa, Argentina. Note great height of trees, bromeliad (*Bromelia* sp.) ground cover. September 18, 1968.

and *Tessaria integrifolia*. Species of *Ficus*, *Phytolacca*, *Inga*, *Piptadenia*, *Pithecolobium*, *Lonchocarpus*, and others comprise the subtropical forest element. Lianas, bamboo groves (fig. 9), and epiphytes are common. This forest has been cut to a considerable extent in places, and selectively cut throughout, often with great waste.

The chaco rivers bear forests dominated by *Piptadenia macrocarpa*, *P. excelsa*, *Pterogyne nitens*, and *Tipuana tipu* in the Tala forest region of the western chaco. Eastwardly, the forests

dwindle rapidly with diminishing rainfall and receding river water. The river courses of the west-central chaco are marked by an impoverished gallery scrub woodland dominated by *Acacia macracantha* and other acacias, which can colonize even river islands that are subjected to strong erosion. Species of *Baccharis* and *Nicotiana* accompany the acacias, which attain a height of 5 m. In the center of the chaco there is no longer a gallery scrub to speak of along the usually dry watercourses of most streams; only



FIG. 8. Pantanal bordering large area of continuous chaco woods (mixed quebracho woods and gallery forest) containing much bamboo (*Guadua*) near Paraguay River, vicinity of Payagua, 55 km. SE of Formosa (city), Argentina. September 25, 1968.



FIG. 9. Bamboo (*Guadua* sp.) groves among mixed, recently burned pantanal and gallery forest-chaco woodland remnants near Paraguay River 55 km. SE of Formosa (city), Argentina. September 27, 1968.

the Bermejo, the Pilcomayo, and parts of a few others carrying some water retain a semblance of gallery scrub vegetation. At the eastern ends of these rivers dense, tall woods recur, continuous with the gallery forest of the Paraguay River.

Many bird species penetrate the chaco no farther than the gallery forests along the Paraguay-Parana river, the lower reaches of the Pilcomayo and a few other rivers, or these rivers at the western edge of the chaco.

THE PLANT FORMATIONS SURROUNDING THE CHACO

The chaco on the west is bordered by subtropical forest occurring along the Andes south at least as far as Tucumán. I have noted above the gradation of Tala-Mistol woodland with the taller, broader-leaved subtropical forest in the west. It is important to note that in much of the chaco (e.g., Formosa-Salta) one can pass from the open pantanal west to the Andes in continuous, unbroken woodland of the types discussed above, without a clearing except around buildings and villages.

The northwestern limit of the chaco occurs in the hills and lowlands of central Santa Cruz. Here, between the drainage of the Paraguay (Parana) and Guapore (Amazon) rivers, the Amazonian forest, Andean subtropical forest, elements of the Campo Cerrado of Brazil, and the chaco meet. Chaco elements include species of *Prosopis*, *Pithecolobium scalare*, and *Geoffroea decorticans* (Hueck, 1966) in the drier woodlands. Human activities in this region are favoring chaco elements at the expense of more mesic plants.

In the northeast, the chaco east of the pantanal in Mato Grosso presumably gives way directly to Campo Cerrado vegetation. This corner of Mato Grosso is very little known ornithologi-

cally. Information regarding the avifauna and ecology of Mato Grosso are contained in Naumburg (1930) and Fry (1970). Apparently chaco vegetation is not known in eastern Paraguay, although pantanal occurs there and certain chaco birds extend into eastern Paraguay. It seems likely that southeastern Paraguay contains some chaco dry woodland, as does western Corrientes, where chaco and subtropical moist forest meet ecotonally within and especially at the edges of gallery forest (Short, 1971b). Away from the rivers, chaco and pampas form an ecotone where esteros (see fig. 2) permit their contact (e.g., within 10 to 20 km. south of the Upper Parana River in northwestern Corrientes). In northwestern Entre Ríos and central Santa Fe pampas-chaco ecotone is prevalent, although much of the region is highly modified by cultivation. There is evidence from avian distribution suggesting the former occurrence of chaco woodlands east to eastern Entre Ríos and northwestern Uruguay.

An extension of the chaco, which might be designated as chaco scrub (fig. 10), occurs along the western border of the pampas from northern Córdoba south through eastern La Pampa and western Buenos Aires, to the coast (near Bahía Blanca) in southwestern Buenos Aires and north-eastern Río Negro (see Short, 1968, fig. 5). Containing a vastly reduced number of species and usually less than 5 m. high, this formation fundamentally is a depauperate chaco woodland (some Andean steppe shrubs also occur). However, few species of birds occupy this scrub as an extension of the chaco. Also, it is cooler than the chaco, and lacks characteristic plants such as most cacti, palms, and other trees and shrubs. It is uncertain whether this represents a recent extension of certain chaco elements, or perhaps, more likely, an ancient arm of the chaco dating back to warmer (Tertiary?) times.

SYSTEMATIC ACCOUNTS OF CHACO BIRDS

INTRODUCTION

I have attempted to appraise the taxonomic status of each avian species that breeds in the chaco by giving an evaluation of the variation in each species, its relationships, including wherever

possible the establishment of its closest relatives, and the nature of the relationship. Where superspecies were found (see Short, 1969a; Mayr and Short, 1970), the component allospecies in the chaco is listed following the bracketed name of the earliest described species of the superspecies,

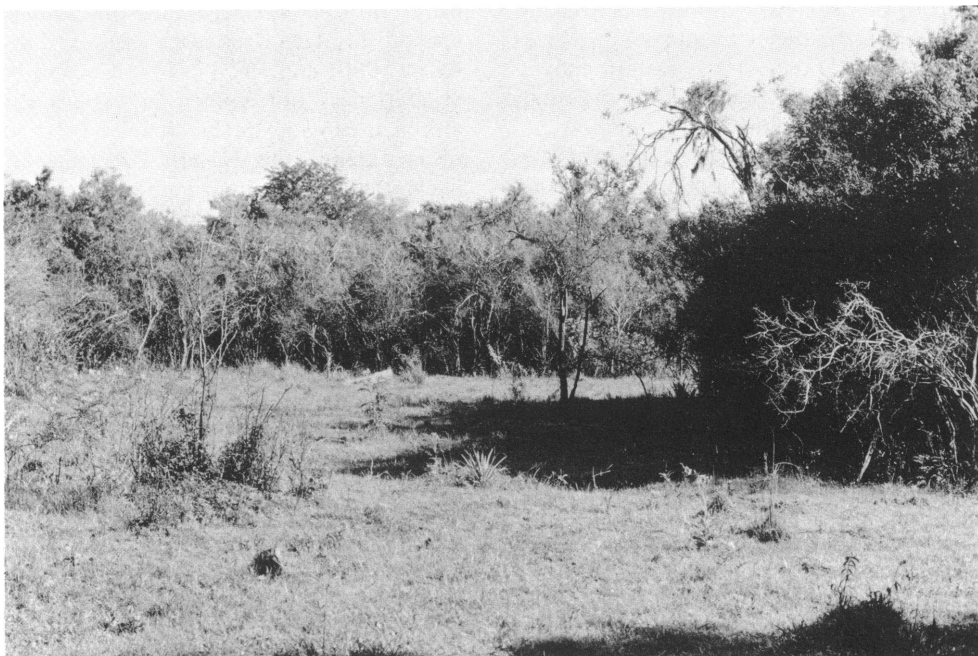


FIG. 10. Low scrub aspect of southeastern edge of chaco near Villa Ana, northern Santa Fe, Argentina. Botanically depauperate version of this woodland, chaco scrub, extends southward from Santa Fe along western border of pampas to southern Buenos Aires (see Short, 1968, fig. 5) and Río Negro. October 2, 1968.

in the manner suggested by Amadon (1966). Wherever more than one allospecies of a single superspecies inhabits the chaco, they are listed after the superspecies and discussed together under one entry in the Systematic Accounts. Asterisks mark polytypic species (see Systematic Accounts). Question marks indicate species inhabiting the fringes of the chaco, and possibly breeding within the chaco, but not yet proved to occur there.

Only those species known to breed or suspected of breeding in the chaco are on this list. Migrant birds obviously have an impact on the evolution of a resident avifauna. In the chaco these effects are not considered to play a major role in determining the species able to breed there. Northern migrants, apt to occur in the chaco during breeding season are few indeed, and most are large nonpasserines, such as shorebirds. The only common wintering northern passerine species is the swallow *Hirundo rustica*. Wintering species from farther south are more numerous, but they appear chiefly during the nonbreeding

period. They may compete with, or prey, to some extent, on resident species, thus directly affecting them. Such effects are outside the scope of this report; their role is yet to be elucidated. The list follows:

FAMILY RHEIDAE

**Rhea americana*

FAMILY TINAMIDAE

**Crypturellus [undulatus] undulatus*

Crypturellus parvirostris

**Crypturellus tataupa*

**Rhynchotus rufescens*

**Nothura [perdicaria] cinerascens*

Nothura boraquira

Nothura [maculosa]

**Nothura maculosa*

**Nothura darwinii*

Eudromia [elegans]

**Eudromia elegans*

**Eudromia formosa*

FAMILY PODICIPEDIDAE

**Podiceps dominicus*

**Podiceps rolland*

- Podiceps major*
 **Podilymbus [podiceps] podiceps*
 FAMILY PHALACROCORACIDAE
 **Phalacrocorax [olivaceus] olivaceus*
 FAMILY ANHINGIDAE
 **Anhinga [anhinga] anhinga*
 FAMILY ARDEIDAE
 **Botaurus [stellaris] pinnatus*
Ixobrychus involucris
 **Tigrisoma lineatum*
 **Nycticorax [nycticorax] nycticorax*
Philherodias pileatus
 **Syrigma sibilatrix*
 **Butorides [virescens] striatus*
 **Egretta [garzetta] thula*
 **Egretta alba*
Ardea [cinerea] cocoi
 FAMILY CICONIIDAE
Mycteria americana
Ciconia maguari
Jabiru mycteria
 FAMILY THRESKIORNITHIDAE
Plegadis [falcinellus] chihi
Harpiprion caeruleus
 **Theristicus caudatus*
 **Phimosus infuscatus*
Platalea ajaja
 FAMILY ANHIMIDAE
Chauna [chavaria] torquata
 FAMILY ANATIDAE
Dendrocygna [bicolor] bicolor
Dendrocygna viduata
 **Dendrocygna autumnalis*
Neochen jubata
Cairina moschata
 **Sarkidiornis melanotos*
Callonetta leucophrys
 **Amazonetta brasiliensis*
 **Anas versicolor*
Netta peposaca
Heteronetta atricapilla
Oxyura dominica
Oxyura vittata
 FAMILY CATHARTIDAE
 **Cathartes aura*
Cathartes burrovianus
 **Coragyps atratus*
Sarcoramphus papa
 FAMILY ACCIPITRIDAE
Leptodon cayanensis
 **Chondrohierax uncinatus*
 **Elanoides forficatus*
 **Gampsonyx swainsonii*
 **Elanus [caeruleus] leucurus*
 **Rostrhamus sociabilis*
- ?*Harpagus diodon*
Ictinia [plumbea] plumbea
 **Geranospiza caeruleus*
Circus buffoni
 **Accipiter [bicolor] bicolor*
 **Accipiter [nisus] striatus*
 **Buteogallus urubitinga*
Harpyhaliaetus [coronatus] coronatus
Heterospizias meridionalis
 **Busarellus nigricollis*
 **Geranoaetus melanoleucus*
 **Parabuteo unicinctus*
 **Buteo nitidus*
 **Buteo magnirostris*
Buteo leucorrhous
 ?**Buteo brachyurus*
 **Buteo [albicaudatus] albicaudatus*
 ?*Harpia harpyja*
Spizastur melanoleucus
 **Spizaetus ornatus*
 FAMILY FALCONIDAE
 **Polyborus plancus*
Polyborus [chimachima]
Polyborus chimachima
 **Polyborus chimango*
Herpetotheres cachinnans
 **Micrastur [ruficollis] ruficollis*
 **Micrastur semitorquatus*
Spiziateryx circumcinctus
 **Falco [tinnunculus] sparverius*
 **Falco rufigularis*
 **Falco femoralis*
Falco [peregrinus] deiroleucus
 FAMILY CRACIDAE
 **Ortalis canicollis*
 **Penelope [obscura] obscura*
 **Aburria [pipile] pipile*
 **Crax [rubra] fasciolata*
 FAMILY ARAMIDAE
 **Aramus guarauna*
 FAMILY RALLIDAE
 **Rallus [nigricans] sanguinolentus*
 **Rallus maculatus*
 **Aramides cajanea*
Aramides ypecaha
 **Porzana albicollis*
 **Poliolimnas flaviventer*
 **Neocrex erythrops*
 **Porphyriops melanops*
 **Laterallus melanophaius*
 **Gallinula chloropus*
Porphyryula martinica
Porphyryula flavirostris
Fulica armillata
Fulica [atra] leucoptera
Fulica rufifrons

FAMILY CARIAMIDAE

Cariama cristata
Chunga burmeisteri

FAMILY JACANIDAE

**Jacana [spinosa] jacana*

FAMILY ROSTRATULIDAE

Nycticryphes semicollaris

FAMILY CHARADRIIDAE

**Vanellus [chilensis] chilensis*
Vanellus cayanus
Charadrius collaris

FAMILY SCOLOPACIDAE

**Gallinago [gallinago] gallinago*
?**Gallinago undulata*

FAMILY RECURVIROSTRIDAE

Himantopus [himantopus] melanurus

FAMILY LARIDAE

**Larus [cirrocephalus] cirrocephalus*
**Phaetusa simplex*
Sterna [albifrons] superciliaris

FAMILY RYNCHOPIDAE

**Rynchops [nigra] nigra*

FAMILY COLUMBIDAE

Columba [speciosa] speciosa
**Columba [corensis] picazuro*
**Columba maculosa*
**Columba cayennensis*
**Zenaida [macroura] auriculata*
**Columbina squammata*
**Columbina minuta*
**Columbina talpacoti*
**Columbina [picui] picui*
Claravis pretiosa
**Leptotila [verreauxi] verreauxi*

FAMILY PSITTACIDAE

**Ara ararauna*
Ara chloroptera
Ara [maracana] auricollis
**Aratinga acuticauda*
**Aratinga [leucophthalmus] leucophthalmus*
**Aratinga [canalicularis] aurea*
Aratinga nenday
**Pyrrhura molinae*
Pyrrhura [frontalis]
**Pyrrhura frontalis*
Pyrrhura devillei
**Myiopsitta monachus*
? *Forpus [passerinus] xanthopterygius*
**Brotogeris versicolurus*
**Pionus maximiliani*
**Amazona [aestiva] aestiva*

FAMILY CUCULIDAE

Coccyzus [cinereus] cinereus
Coccyzus [minor] melacoryphus
**Piaya cayana*

Crotophaga major

Crotophaga ani

Guira guira

**Tapera naevia*

**Dromococcyx pavoninus*

FAMILY TYTONIDAE

**Tyto [alba] alba*

FAMILY STRIGIDAE

**Otus [choliba] choliba*
**Bubo [bubo] virginianus*
?**Pulsatrix perspicillata*
**Glaucidium minutissimum*
**Glaucidium [brasilianum] brasilianum*
**Athene cunicularia*
?**Ciccaba [huhula] huhula*
Strix hylophila
**Strix rufipes*
**Asio clamator*
**Asio flammeus*

FAMILY NYCTIBIIDAE

**Nyctibius griseus*

FAMILY CAPRIMULGIDAE

**Caprimulgus [carolinensis] rufus*
?**Caprimulgus cayennensis*
**Caprimulgus parvulus*
**Hydropsalis brasiliana*
Eleothreptus anomalus
**Podager nacunda*
?**Chordeiles acutipennis*
**Lurocalis semitorquatus*

FAMILY APODIDAE

?*Cypseloides [niger] rothschildi*
**Chaetura andrei*

FAMILY TROCHILIDAE

?*Phaethornis [pretrei] pretrei*
? *Phaethornis subochraceus*
**Eupetomena macroura*
Colibri serrirostris
Anthracothorax [nigricollis] nigricollis
**Chlorostilbon aureoventris*
?**Thalurania furcata*
Hylocharis sapphirina
Hylocharis chrysura
**Polytmus guainumbi*
**Amazilia chionogaster*
Helimaster furcifer

FAMILY TROGONIDAE

**Trogon rufus*
**Trogon surrucura*
**Trogon curucui*

FAMILY ALCEDINIDAE

**Ceryle [alcyon] torquata*
**Chloroceryle amazona*
**Chloroceryle americana*

FAMILY MOMOTIDAE

**Momotus momota*

FAMILY BUCCONIDAE

?**Notharchus macrorhynchus*

**Nystalus maculatus*

FAMILY RAMPHASTIDAE

?**Pteroglossus [aracari] castanotis*

Ramphastos dicolorus

**Ramphastos toco*

FAMILY PICIDAE

**Picumnus [cirratus] cirratus*

**Picoides [mixtus] mixtus*

Melanerpes candidus

Melanerpes cactorum

**Veniliornis [passerinus] passerinus*

**Piculus [chrysochloros] chrysochloros*

**Colaptes [punctigula] melanochloros*

**Colaptes campestris*

**Celeus [elegans] lugubris*

Dryocopus [pileatus]

**Dryocopus lineatus*

Dryocopus schulzi

**Campephilus [melanoleucos] melanoleucos*

**Campephilus leucopogon*

FAMILY DENDROCOLAPTIDAE

**Sittasomus griseicapillus*

Drymornis bridgesi

**Xiphocolaptes major*

Dendrocolaptes [picumnus]

**Dendrocolaptes picumnus*

**Dendrocolaptes platyrostris*

**Lepidocolaptes angustirostris*

**Campylorhamphus [trochilirostris]*

trochilirostris

FAMILY FURNARIIDAE

**Upucerthia [certhioides] certhioides*

**Furnarius rufus*

Furnarius cristatus

Leptasthenura platensis

**Schoeniophylax phryganophila*

**Synallaxis [azarae] frontalis*

**Synallaxis albescens*

**Synallaxis scutatus*

**Certhiaxis pyrrhophia*

**Certhiaxis cinnamomea*

**Thripophaga [pyrrholeuca] baeri*

Phacellodomus [rufifrons]

**Phacellodomus rufifrons*

Phacellodomus sibilatrix

Phacellodomus ruber

**Phacellodomus striaticollis*

**Phleocryptes melanops*

Coryphistera alaudina

**Anumbius annumbi*

**Pseudoseisura lophotes*

**Pseudoseisura cristata*

**Philydor rufosuperciliatus*

FAMILY FORMICARIIDAE

**Batara cinerea*

**Taraba major*

**Thamnophilus doliatus*

**Thamnophilus [caerulescens] caerulescens*

?**Thamnophilus [ruficapillus] ruficapillus*

Myrmorchilus strigilatus

**Herpsilochmus pileatus*

?**Formicivora rufa*

?*Pyriglena [leucoptera] leuconota*

FAMILY RHINOCRYPTIDAE

Rhinocrypta lanceolata

**Melanopareia [torquata] maximiliani*

FAMILY COTINGIDAE

Attila phoenicurus

Casiornis [rufa] rufa

**Xenopsaris albinucha*

**Pachyramphus viridis*

**Pachyramphus polychopterus*

**Platypsaris rufus*

**Tityra cayana*

**Tityra inquisitor*

FAMILY TYRANNIDAE

**Xolmis [cinerea] cinerea*

**Xolmis irupero*

Xolmis dominicana

Gubernetes yetapa

?*Alectrurus tricolor*

Alectrurus [Yetapa] risora

**Knipolegus aterrimus*

Knipolegus [cyanirostris]

Knipolegus cyanirostris

?*Knipolegus cabanisi*

Knipolegus [Entotriccus] striaticeps

**Hymenops perspicillata*

**Fluvicola [nengeta] pica*

Fluvicola leucocephala

**Pyrocephalus rubinus*

Satrapa icterophrys

**Machetornis rixosus*

**Tyrannus savanna*

**Tyrannus [melancholicus] melancholicus*

**Empidonomus varius*

**Empidonomus aurantioatrocristatus*

**Legatus leucophaius*

**Megarhynchus pitangua*

**Myiodynastes maculatus*

**Pitangus sulphuratus*

**Myiarchus ferox*

**Myiarchus [crinitus] tyrannulus*

**Myiarchus swainsonii*

**Contopus [virens] cinereus*

**Empidonax [albigularis] eulerei*

- **Cnemotriccus fuscatus*
 **Myiophobus [fasciatus] fasciatus*
 **Hirundinea ferruginea*
 **Tolmomyias sulphureus*
 **Todirostrum margaritaceiventer*
 **Euscarthmus meloryphus*
Pseudocolopteryx [acutipennis] dinellianus
Pseudocolopteryx sclateri
Pseudocolopteryx flaviventris
 **Polystictus [pectoralis] pectoralis*
Culicivora caudacuta
 **Stigmatura [budytoides] budytoides*
 **Serpophaga subcristata*
Serpophaga [nigricans] nigricans
Inezia [inornata] inornata
 **Elaenia [martinica] flavogaster*
 **Elaenia spectabilis*
Elaenia [albiceps] parvirostris
Elaenia [mesoleuca] mesoleuca
Suiriri [suiriri] suiriri
 **Sublegatus modestus*
 **Phaeomyias murina*
 **Camptostoma [obsoletum] obsoletum*
- FAMILY PHYTOTOMIDAE
 **Phytotoma [rutila] rutila*
- FAMILY HIRUNDINIDAE
Tachycineta [albiventer] albiventer
Tachycineta [leucorrhoa] leucorrhoa
 **Phaeoprogne tapera*
Progne [subis]
 **Progne chalybea*
 **Progne modesta*
Stelgidopteryx fucata
 **Stelgidopteryx ruficollis*
- FAMILY CORVIDAE
Cyanocorax [caeruleus] cyanomelas
 **Cyanocorax [chrysops] chrysops*
- FAMILY TROGLODYTIDAE
 **Cistothorus [platensis] platensis*
 ?*Thryothorus [guarayanus] guarayanus*
 **Troglodytes aedon*
- FAMILY MIMIDAE
 **Mimus [saturninus] saturninus*
Mimus [triurus] triurus
 **Donacobius atricapillus*
- FAMILY TURDIDAE
 **Turdus rufiventris*
 **Turdus leucomelas*
Turdus amaurochalinus
- FAMILY SYLVIIDAE
 **Polioptila dumicola*
- FAMILY MOTACILLIDAE
 **Anthus lutescens*
- FAMILY VIREONIDAE
 **Cyclarhis gujanensis*
- **Vireo [olivaceus] olivaceus*
- FAMILY ICTERIDAE
 **Molothrus bonariensis*
Molothrus rufoaxillaris
 **Molothrus badius*
Sturnella [militaris] superciliaris
 **Agelaius ruficapillus*
 **Agelaius cyanopus*
Agelaius flavus
Pseudoleistes guirahuro
Pseudoleistes virescens
Amblyramphus holosericeus
 **Gnorimopsar chopi*
 **Icterus icterus*
 **Icterus [cayanensis] cayanensis*
Cacicus [chrysopterus] chrysopterus
Cacicus solitarius
 **Cacicus [haemorrhous] haemorrhous*
 **Psarocolius decumanus*
- FAMILY PARULIDAE
 **Parula americana*
 **Geothlypis [aequinoctialis] aequinoctialis*
Basileuterus [flaveolus] flaveolus
 **Basileuterus [culicivorus] culicivorus*
Basileuterus hypoleucus
Basileuterus leucoblepharus
 **Conirostrum speciosum*
- FAMILY THRAUPIDAE
 **Tersina viridis*
 ?**Chlorophonea cyanea*
 **Euphonia [musica] musica*
 **Euphonia chlorotica*
 **Thraupis [sayaca] sayaca*
 **Thraupis bonariensis*
 **Piranga [rubra] flava*
Tachyphonus [rufus] rufus
 **Nemosia pileata*
 ?**Hemithraupis [guira] guira*
 **Thlypopsis [sordida] sordida*
 ?**Cissopis leveriana*
- FAMILY EMBERIZIDAE
Saltator [coerulescens]
 **Saltator coerulescens*
 **Saltator similis*
 **Saltator [aurantiiostris] aurantiiostris*
Gubernatrix cristata
Paroaria [dominicana] coronata
 **Paroaria [gularis] capitata*
 **Pheucticus [chrysopeplus] aureoventris*
 **Cyanocompsa [cyanea] cyanea*
 **Volatinia jacarina*
 **Sporophila collaris*
 **Sporophila lineola*
 **Sporophila caerulescens*

- **Sporophila leucoptera*
- Sporophila hypoxantha*
- ?*Sporophila [cinnamomea] hypochroma*
- **Sicalis flaveola*
- **Sicalis luteola*
- Lophospingus pusillus*
- **Coryphospingus [cucullatus] cucullatus*
- **Arremon [taciturnus] flavirostris*
- **Ammodramus [humeralis] humeralis*
- **Aimophila strigiceps*
- **Junco capensis*
- **Coryphaspiza melanotis*
- **Emberizoides [herbicola] herbicola*
- **Emberizoides ypiranganus*
- **Embernagra [platensis] platensis*
- Donacospiza albifrons*
- **Poospiza [torquata] torquata*
- Poospiza [melanoleuca] melanoleuca*
- **Poospiza nigrorufa*
- Saltatricula multicolor*

FAMILY CARDUELIDAE

- **Carduelis [magellanica] magellanica*

SPECIES ACCOUNTS

Every species of bird known to breed or suspected of breeding (latter shown with question mark in list above) in the chaco is treated below in the same order as on the list. Taxonomy, ecology, and distribution (or distribution and variation for polytypic species) are discussed. The order of species generally follows that of Meyer de Schauensee (1966; also the source of much of the distributional data); changes from that classification are documented below. That treatise also contains citations and authors of scientific names used herein.

The taxonomy section contains a statement of whether the species is considered polytypic, which is followed by a more or less detailed discussion or a simple statement of the known or suspected relationships of the species; of course such information is not available for every species. If the species is an allospecies of a superspecies, the other allospecies comprising the superspecies are mentioned, their ranges indicated, and their characteristics noted, as well as whether secondary contacts are known to occur (if the allospecies and secondary contacts are outside of South America, the information presented is kept to a minimum). Fossils, if known from

South America, are mentioned. Generic monotypy relates to neospecies of a genus, without regard for paleospecies.

Aspects of ecology thought to be useful for nonspecialists in South American birds are mentioned in the "ecology" section. Data important in avian distribution, such as preferred habitats, food items, mode and site of foraging, site of nest, and whether the species is migratory are stressed. Even some of these rudimentary data are lacking for many South American species. The information presented is based on personal observations wherever possible, and those features of ecology of the birds (populations, subspecies) inhabiting the chaco are emphasized over those perhaps differing elsewhere. The information is not meant to be complete, or to apply to all populations of the species.

The "distribution" section contains an initial brief statement of the range of the species (N, S, E, W, and combinations thereof, refer to compass directions, as east, but not eastern, southeast, but not southeastern), and particularly whether the species is endemic in South America. This is followed by a "capsule" description, emphasizing its South American range. Finally, the occupied parts of the chaco are noted, and mention is made of where the chaco is in relation to the overall distribution of the species, e.g., whether it is at the border of the species' range. Disjunctions in range are stressed. For polytypic species I call this section "distribution and variation." It begins with the brief statement of range and endemism, followed by a capsule description of the species' distribution. Depending on the nature and complexity of the variation, the range(s) of the subspecies occupying the chaco is described, and its major features are stated. When a species is comprised of only two recognized subspecies, or sometimes three, each of these may be mentioned and characterized, particularly if they intergrade with, or otherwise meet, a race inhabiting the chaco, or if they occupy disjunct ranges. The characterization of the subspecies is meant to give the reader some idea of the nature of the variation. Very strongly differentiated races or racial groups are often treated in some detail, particularly if disjunct ranges are involved, or if secondary intergradation occurs (even outside the chaco).

FAMILY RHEIDAE

Rhea americana

Greater Rhea

Figure 11

Taxonomy. Genus monotypic, species polytypic. One Pleistocene paleospecies of *Rhea* is known (Brodkorb, 1963). Rheas are known as fossils since the Eocene, *Rhea* itself since Lower Pleistocene. The fossils mainly come from Argentina, including Patagonia, but also from Minas Gerais.

Ecology. Flightless, sedentary. Rheas occupy more or less open country, and presumably have done so throughout the Tertiary. However, they

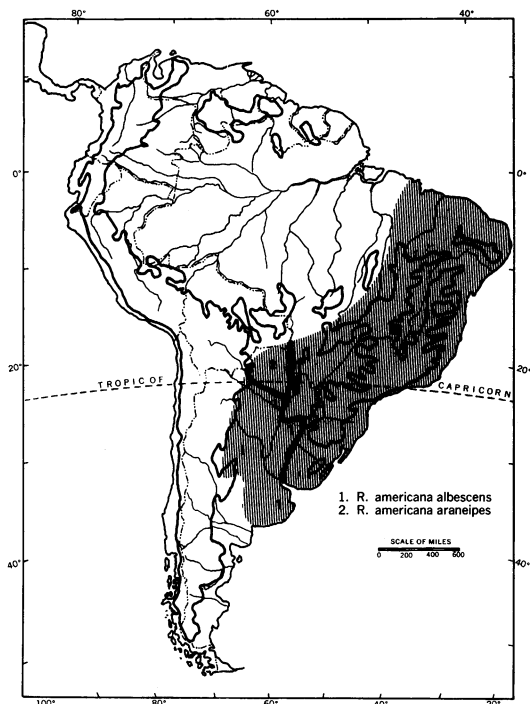


FIG. 11. Range of Greater Rhea (*Rhea americana*). Only subspecies found within chaco have ranges delineated here. *Rhea americana* is most common and continuously distributed within chaco along eastern edge in pantanal. The race *araneipes* is almost restricted to northern chaco. Distribution in campo-pampas but tolerates more open woodland. Dark line very approximately borders upland areas above about 1200 feet in elevation.

are not exclusively open grassland birds, for the Greater Rhea also inhabits woodland edges, savannas, and edges of cultivated lands (where not excessively hunted). This species may be excluded from Patagonia and the Andean highlands by the Darwin's Rhea (*Pterocnemia pennata*), the only other extant species of Rheidae, with which *R. americana* may compete.

Distribution and variation. Endemic in South America, E and S of Amazonia. Fully occupies the chaco in suitable open areas, extending beyond in all directions but mainly NE through campo, caatinga, and southeastern Brazilian forests (in clearings) to the Atlantic Coast as far N as Maranhão; also S to Patagonia (northern border), and W to Andean foothills. Range essentially continuous. Several races of *americana* have been described on the basis of minor size and color variation. Some of the variation is clinal, southwestern birds tending to be larger and darker. Chaco populations are assigned to *R. americana albescens* (southern chaco and to W, S, and E) and to *R. a. araneipes* (western Paraguay, southwestern Mato Grosso), both of which extend beyond the chaco.

FAMILY TINAMIDAE

Crypturellus undulatus

Undulated Tinamou

Figure 12

Taxonomy. Polytypic. Forms superspecies with the northern allospecies *C. cinnamomeus*. Ancestral [*undulatus*] probably gave rise to *undulatus* in Amazonia or about the fringes of Amazonia and to *cinnamomeus* as a northern offshoot. *Crypturellus cinnamomeus* closely resembles *C. undulatus* in bill shape, ventral coloration, and in the patterns of variation in dorsal color and barring.

Ecology. Nonmigratory, terrestrial. A forest and forest edge species. The genus is essentially tropical in distribution. The northern allospecies *cinnamomeus* is a xeric woodland species. *Crypturellus undulatus* seems ecologically more tolerant; however, it does not fully occupy the xeric chaco or caatinga, possibly because of competition from tinamous (*Rhynchotus*, *Nothura*, *Eudromia*), which are more xeric adapted but do not occur in the range of *cinnamomeus*.

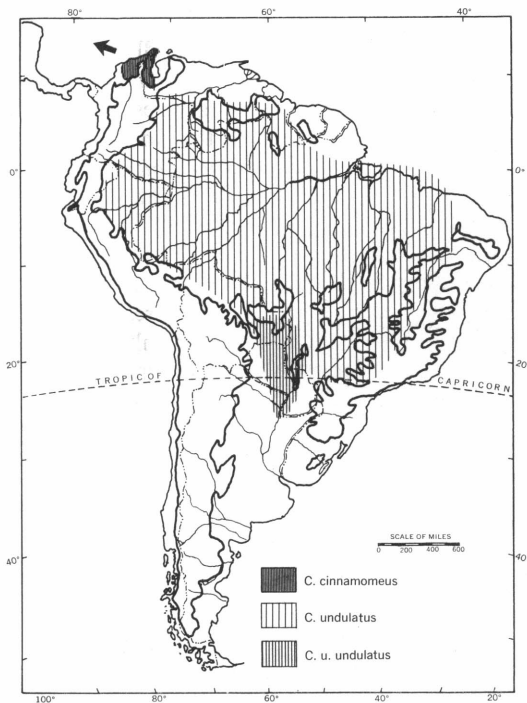


FIG. 12. Range of Undulated Tinamou (*Crypturellus undulatus*). South American range of its allospecies *C. cinnamomeus* also is shown. Distribution of *undulatus*, mainly Amazonian, reaches its southern limit in northeastern chaco. Isolate of essentially Middle American *cinnamomeus* in arid Venezuela and Colombia, and chaco occurrence of *undulatus* indicate xeric tolerance for this superspecies of forest tinamou. Arrow indicates range extends northward.

Distribution and variation. Endemic in South America, essentially in Amazonia. The northeastern chaco forms the southern extreme of the range of continuously distributed *undulatus*, which extends NW to eastern Peru and eastern Ecuador, N to the Meta and upper Orinoco rivers and the Guianian highlands, NE to the mouth of the Amazon, and E to the Brazilian highlands and western caatinga. *Crypturellus cinnamomeus*, not sympatric with *undulatus*, occurs discontinuously from northern Venezuela to Mexico. A number of subspecies of *C. undulatus* have been described on the basis of variation in color and in pattern. Populations reaching the northern chaco are assigned to *C. u. undulatus*, distinct by virtue

of its strong dorsal barring; other races have the barring reduced or obsolete, but there is clinal variation with Peruvian populations.

Crypturellus parvirostris
Small-billed Tinamou

Taxonomy. Monotypic. Appears not particularly closely related to any other species of *Crypturellus*. Fossil from the Pleistocene of Minas Gerais.

Ecology. Nonmigratory, terrestrial. A tinamou of the forest and forest edges.

Distribution. Endemic in east-central South America. Reaches the limit of its range in the northern pantanal and eastern (moist) dry chaco woodland of Santa Cruz, the eastern portion of western Paraguay and southwestern Mato Grosso. Extends NW to eastern Peru, N to the Amazon, E to the Atlantic Coast from Pará S to São Paulo, and S to east-central Paraguay and Misiones.

Crypturellus tataupa
Tataupa Tinamou

Taxonomy. Polytypic. Closest relative among species of *Crypturellus* is uncertain.

Ecology. Nonmigratory, terrestrial. A forest, forest edge, and brushland species.

Distribution and variation. Endemic in South America, S of Amazonia. Occurs throughout the chaco and slightly beyond it to the S and W, and NW to eastern Peru, N to northern Mato Grosso and Maranhão, E to the Atlantic Coast, S to Rio Grande do Sul and Córdoba and northern San Juan, Argentina, and W to the Andean subtropical forests. Occupies the entire south-central portion of the species range, from eastern Bolivia and the Andes E to eastern Mato Grosso, Espírito Santo, and Rio Grande do Sul. Moderate size and minor color variation mark the several, moderately defined subspecies.

Rhynchotus rufescens
Rufous-winged Tinamou
Figure 13

Taxonomy. Polytypic species, genus monotypic. No close relatives. Known as fossil from Minas Gerais (Pleistocene).

Ecology. Nonmigratory, terrestrial. Favors deep grass, brushy areas, and woodland edges.



FIG. 13. Range of Rufous-winged Tinamou (*Rhynchotus rufescens*). A race occurs west of chaco, isolated from populations east and north. Distribution mainly campo-pampas, but very tolerant of forest, where it occurs at edges and openings.

Distribution and variation. Endemic in central and south-central South America. Occurs in moist parts of the chaco, in the E, questionably in western Paraguay, and possibly in the western fringes. Its range extends S to the Tucumán region in the W, and in the E beyond the chaco to Río Negro. The species extends NW from the chaco to northern Bolivia and to the Rio Madeira, to the lower Amazon, NE to central Maranhão and Bahía, E to Rio de Janeiro and the Atlantic Coast S of there, S to Uruguay and Río Negro, and W to the Andean foothills of southern Bolivia and northwestern Argentina. *Rhynchotus rufescens pallescens* occupies the southeastern chaco in the pantanal region, and extends S to Río Negro; it is confined to the pantanal in the northern part of its range (Paraguay). The smaller *R. r. rufescens* occurs in southwestern Mato Grosso, Santa Cruz, and the western chaco border, perhaps entering the chaco

in northwestern Argentina and western Paraguay, as well as the northern border of Paraguay and possibly elsewhere in the Paraguayan chaco. The species can be divided into an eastern and northern (*rufescens*) group, and the submontane western *maculicollis*, which differs markedly in dorsal pattern and especially in having the neck streaked. Among the three races of the *rufescens* group, *pallescens* is distinctly larger than the other forms, with which it appears to intergrade.

Nothura cinerascens
Brushland Tinamou
Figure 14

Taxonomy. Polytypic species. The genus *Nothoprocta*, in which this species is usually placed, is considered congeneric with *Nothura*, the merger being necessary to make the genus monophyletic; that is, various "*Nothoprocta*" species appear independently derived from *Nothura*, and are hence more distantly related to each other than each is to *Nothura sensu stricto* (examples are "*Nothoprocta*" *curvirostris*, probably related to *Nothura maculosa*, and *N. [perdicaria]*, which appears related to *Nothura boraquira*). A paleospecies of *Nothura*, *N. paludosa*, is known from the Upper Pleistocene of Buenos Aires (Brodkorb, 1963). *Nothura perdicaria* of Chile and *N. pentlandii* of Andean Ecuador to Argentina are allopatric with *N. cinerascens*; they are similar in details of pattern, including that of the remiges, and differ mainly in body size, size of bill, and minor color features. I consider these three species to comprise a super-species.

Ecology. Nonmigratory, terrestrial. A common tinamou restricted to dry woodlands, brushland, and their edges.

Distribution and variation. Endemic in south-central South America, superspecies also endemic in South America. Restricted in its distribution to the chaco and adjacent brushland to the S and SW. Does not reach the northern chaco border or the portions E of the Paraguay-Parana rivers. Extends from southern Bolivia and the north-central Paraguayan chaco S to Mendoza in the SW and Río Negro in the SE; E to the Paraguay River, and to the Parana River in the N, but only to western Santa Fe, Córdoba, La Pampa, and southern Buenos Aires in the S; and W to the Andean foothills and arid valleys. Two, not well

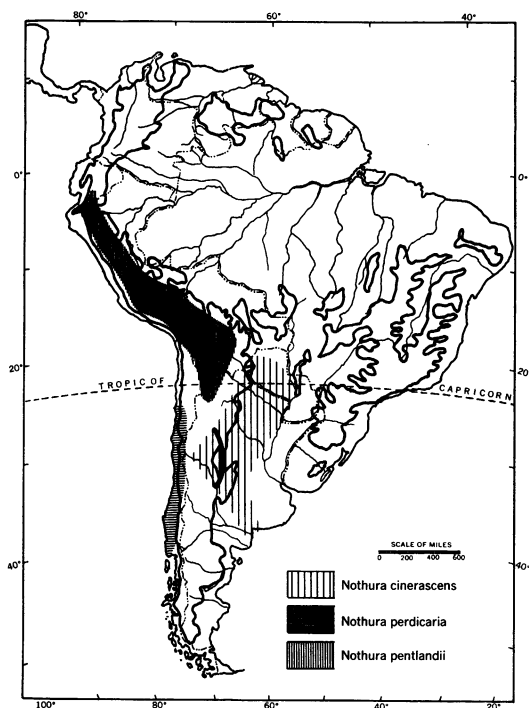


FIG. 14. Range of Brushland Tinamou (*Nothura cinerascens*), and other allospecies of superspecies *N. perdicaria*. Distribution of *cinerascens* is chaco-chaco scrub-subtropical dry forest, contrasting with Andean *pentlandii* and Fuegian (Chilean) *perdicaria*. Dark line denotes approximate border between weak races *N. c. parvimaculata* of La Rioja region, and *N. c. cinerascens*, occupying remainder of range.

marked (small size and color differences) races, *N. c. cinerascens* occupying the chaco portion of the species' range, and indeed all but the southwestern corner of that range, and *parvimaculata* in the La Rioja region of Argentina.

Nothura boraquira
White-breasted Tinamou
Figure 15

Taxonomy. Monotypic. This tinamou seems related to the *N. perdicaria* group (see above). The disjunct populations are but slightly differentiated and have not been racially separated.

Ecology. Nonmigratory, terrestrial. A dry brushland and woodland tinamou.

Distribution. Endemic in central South America. Disjunct populations occur in the northern

chaco and in the caatinga region. The chaco disjunct is limited to western Paraguay and Santa Cruz. The caatinga disjunct occurs in Piauí, Ceará, Bahia, and Minas Gerais. These forms are weakly differentiated (slight, average color differences), and appear to have been connected in the recent past.

Nothura maculosa
Spotted Nothura and
Nothura darwini
Darwin's Nothura
Figure 16

Taxonomy. Both polytypic. These species are largely allopatric, with ecological separation even within the zone of overlap. *Nothura darwini* is a smaller-footed species, rustier generally, and with breast streaks broadened by a border of chestnut or rufous about the darker central streaks.

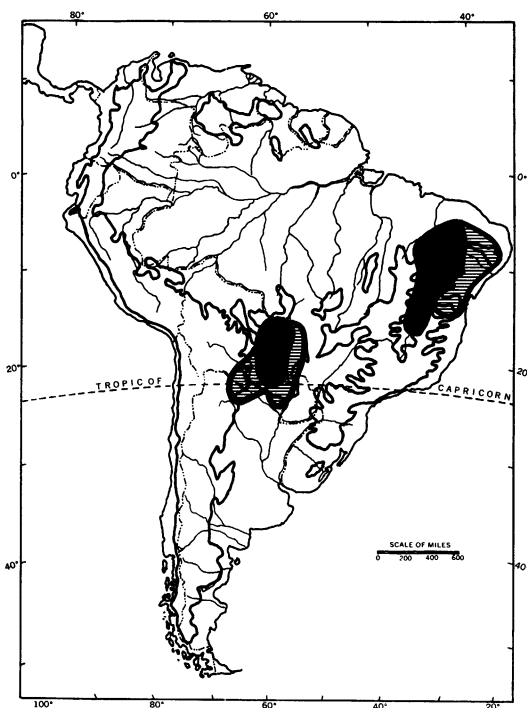


FIG. 15. Range of White-breasted Tinamou (*Nothura boraquira*) shown in black, and of Stripe-backed Antbird (*Myrmorchilus strigilatus*), indicated by horizontal lines. Distributions with chaco and caatinga isolates of each species, in both cases weakly differentiated and probably not racially separable.

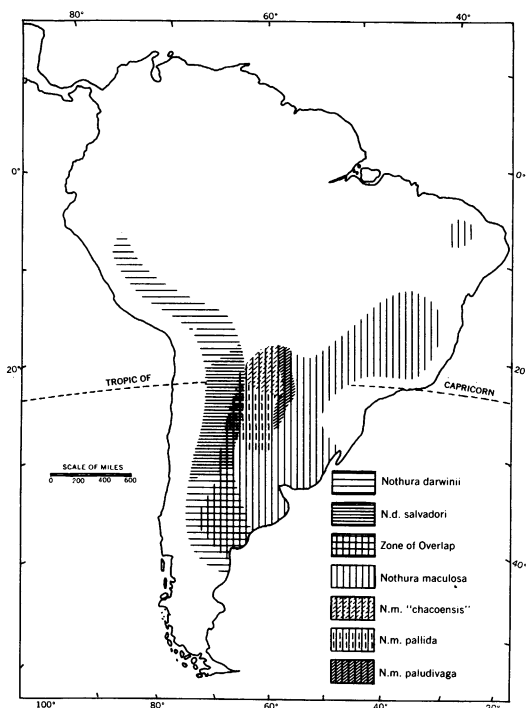


FIG. 16. Range of Spotted Nothura (*Nothura maculosa*) shown with vertical lines and Darwin's Nothura (*N. darwinii*), indicated by horizontal lines. These allopecies comprise a superspecies. Crosshatching denotes their overlap areas (different subspecies of each are involved in various regions). Chaco-occurring subspecies of each allopecies are indicated. *Nothura maculosa* shows a pampas-chaco-caatinga distribution, whereas *N. darwinii* is essentially Andean. *Nothura maculosa* is only species having three subspecies virtually confined to chaco, including problematical "chacoensis." An isolate of *N. maculosa* occurs in the northern caatinga.

Nothura maculosa is larger-footed, browner, grayer, or buffier generally, with simple dark brown breast streaks. *Nothura maculosa* has fully or almost fully barred remiges; *N. darwinii* has reduced barring especially on the outermost primaries, which either lack bars or have a few basally only. The status of *N. maculosa chacoensis* is not resolved. This form, usually treated as a species, is allopatric with adjacent races; there are indications of intergradation with *N. m. paludivaga* in the eastern Paraguayan chaco, although series are not available for the analysis of the inter-

breeding. I have examined the type of *chacoensis* and specimens in various museums, including the Senckenberg Museum in Frankfurt and the Koenig Museum in Bonn, Germany, as well as several major museums in the United States. *Nothura maculosa chacoensis* is smaller than other races of *N. maculosa*, except *cearensis*; its middle toe is shorter (24 to 26 mm.) than that of adjacent *paludivaga* (27 to 30 mm.). It is buffier, paler, and less gray above and less blackish also because the dorsal black bars are very fine, and narrower bars of *paludivaga* are vermiculate in *chacoensis*. Otherwise, I can find no trenchant differences; certainly those observed are minor compared with differences between *N. darwinii* and *N. maculosa*. *Nothura maculosa chacoensis* is heavily barred on its remiges, the ventral streaks are simple, and the color and pattern generally are similar to those of the browner races (e.g., *maculosa*) of *N. maculosa*. The form *chacoensis* appears striking chiefly because it is adjacent to the very dark *N. m. paludivaga*. Like other races of *maculosa*, *chacoensis* varies greatly in the pattern of its markings, although not in its buffy tone. The occurrence of color phases in *Nothura minor* (which *chacoensis* does not approach in any marked way), and the great individual variation in *N. maculosa* and *N. boraquira* suggest that the color pattern differences shown by *chacoensis* are not of the order of species differences in this genus (see Conover, 1950).

Ecology. *Nothura maculosa* is an abundant, small tinamou of open country, including cultivated areas and grasslands, savannas, open woodland (chaco), and clearings in forests along their edges. *Nothura darwinii* frequents open areas in dry woodland, scrub deserts, barren mountain slopes, and Patagonian brushland. They are very sedentary and territorial and forage terrestrially for insects and seeds. Like all tinamous, males incubate and care for the young; the nest is placed on the ground.

Distribution and variation. The superspecies is endemic in South America. *Nothura darwinii* occurs along the eastern slopes of the Andes from central Peru through highland Bolivia to Neuquén and Río Negro, Argentina; in Argentina it extends into the lowlands, narrowly in the N to Salta, and western Santiago del Estero, into Córdoba, and, farther S, more extensively, E to La Pampa, southern Buenos Aires, and coastal

Río Negro and Chubut. A race of *N. maculosa* is isolated in Ceará; otherwise the species ranges from Goiás, Minas Gerais, and interior Rio de Janeiro (probably Bahía also) SW to southern Mato Grosso, and through Paraguay to Salta, Santiago del Estero, Córdoba, La Pampa, and Buenos Aires, and from those provinces E across Argentina to Rio Grande do Sul and Uruguay. *Nothura darwinii salvadori* occurs from southern Bolivia to western Córdoba and Mendoza; it enters the western chaco in Salta and Santiago del Estero. It is larger than *boliviana*, the race occurring to the N, and more rufous (less gray), and heavily marked than *darwinii*. *Nothura maculosa chacoensis*, discussed above, inhabits the dry central and western chaco of Paraguay, and adjacent central Formosa. *Nothura maculosa paludivaga* inhabits the pantanal and moist eastern chaco woodland in Paraguay, presumably adjacent Mato Grosso, and possibly easternmost Bolivia, and it extends S in eastern Formosa to eastern Chaco Province and probably northern Santa Fe. This dark race resembles the chaco scrub and scrub desert *N. m. annectens* and *nigroguttata* of the southern pampas, rather than adjacent races to the W (*pallida*, *chacoensis*) or E (*maculosa*). *Nothura maculosa pallida* (Olrog, 1959) inhabits eastern Salta, adjacent southwestern Paraguay (Escalante; specimens in Koenig Museum) and western Formosa, and Santiago del Estero; it probably reaches Santa Fe and northern Córdoba as well. This pale, buffy race is larger than *chacoensis*, and it is more heavily marked dorsally, but less barred on the remiges (outermost primaries about intermediate between other races of *maculosa*, and *N. darwinii*, but it shows no other approach to the latter). *Nothura maculosa pallida* overlaps with *N. darwinii salvadori* in western Santiago del Estero, and Salta, and perhaps in Catamarca and Córdoba (other races of *darwinii* and of *maculosa* overlap in La Pampa, southern Buenos Aires, Río Negro, and Neuquén). Thus, all the chaco except possibly the Bolivian chaco (I note that the type of *N. m. paludivaga* comes from General Diaz, Paraguay, not far from Santa Cruz, Bolivia), and possibly parts of the dry central chaco of Argentina is occupied by one or another race of *N. maculosa* or by *N. maculosa* in sympatry with *N. darwinii*. *Nothura maculosa chacoensis* is confined to the northwestern chaco, *N. m. pallida* ranges only slightly S of the

southwestern chaco, and *N. m. paludivaga* occurs mainly in the eastern chaco. I know of no other species having three distinct subspecies whose distributions lie mostly within the chaco.

Eudromia elegans
Elegant Crested Tinamou and
Eudromia formosa
Quebracho Crested Tinamou
Figure 17

Taxonomy. Both species polytypic. Genus includes only this superspecies; *Tinamotis* seems closely related, has the same basic head and color pattern generally, and probably is congeneric. Not known as fossils. *Eudromia formosa* differs from *E. elegans* in being variegated above, not

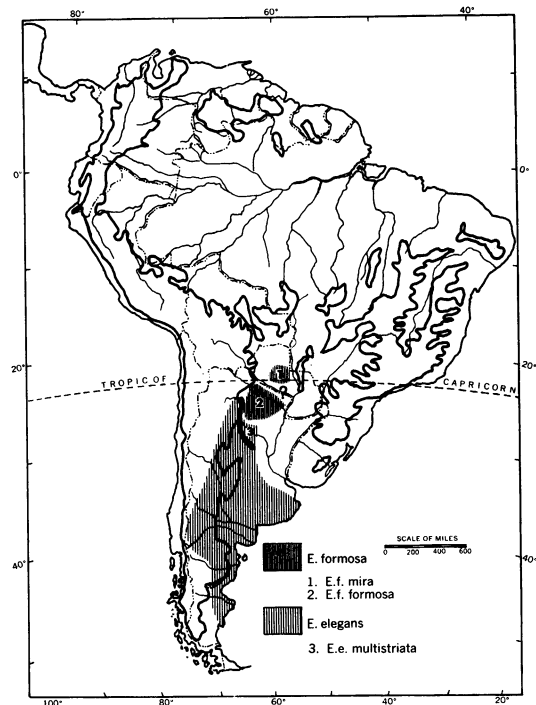


FIG. 17. Range of Elegant Crested Tinamou (*Eudromia elegans*) and Quebracho Crested Tinamou (*E. formosa*) which form a superspecies. *Eudromia formosa* is only endemic chaco bird. These allospecies barely meet and may prove conspecific. Racial contact within *E. formosa* remains to be shown. Distribution of *formosa* is chaco, and of *elegans*, Patagonian-chaco scrub and "monte" zone of Andes.

finely spotted (*E. e. multistriata* is intermediate), in having less complete ventral barring with broader bars (*multistriata* approaches *formosa*), in its unbarred inner remiges, and in the horizontal vermiculations along the breast streaks.

Ecology. Nonmigratory, terrestrial. *Eudromia formosa* is restricted to dry chaco woodland. *Eudromia elegans* occurs in dry chaco woodland and scrub woodland, but seemingly favors more open sites; it extends into the arid western and southern shrub deserts and brushy steppes in Patagonia and along the Andean slopes and also inhabits much of the pampas of Buenos Aires Province. Neither species occurs in the more moist chaco woodlands or very wet pampas or marshland.

Distribution and variation. Superspecies endemic in southern South America. *Eudromia formosa* is restricted to the northern and western chaco. *Eudromia elegans* occupies the southwestern fringe of the chaco, extending NW to the Andean foothills and xeric valleys, E to the more moist eastern chaco woodlands and the pampas of southeastern Buenos Aires, S to the Patagonian coastal region of Chubut and Santa Cruz, and W to the Andean steppes. The two races of *E. formosa*, *E. f. mira* of the Paraguayan chaco and *E. f. formosa* of the Argentine chaco from Formosa and Salta to Santiago del Estero, differ in minor color features; they may meet in northern Formosa. The several races of *E. elegans* fall into two groups, the southern, fine-spotted *elegans* group and the northern, more variegated, less ventrally barred *multistriata* group. *Eudromia elegans multistriata* occurs in Santiago del Estero, and may be in contact with *E. f. formosa* (their interactions are unknown). Although tending toward *formosa* in two features, *multistriata* has the breast streaking and pattern of remiges typical of *E. elegans*.

FAMILY PODICIPEDIDAE

Podiceps dominicus Least Grebe

Taxonomy. Polytypic. Of uncertain relationships within its genus. Known as a fossil from the Pleistocene of Minas Gerais.

Ecology. Water bird, diver, swimmer, nonmigratory. Found on small ponds and larger

lakes, foraging at or beneath the surface; nests on floating mats of vegetation.

Distribution. New World, from Texas and West Indies to Tierra del Fuego, *P. d. speciosus* occurs throughout South America exclusive of Chile and coastal Peru and extends into Middle America. Occurs sporadically where habitat is suitable throughout the chaco, and beyond it in all directions.

Podiceps rolland White-tufted Grebe

Taxonomy. Polytypic. Relationships uncertain within *Podiceps*.

Ecology. Water bird, diver, nonmigratory. Nests on floating vegetation in larger ponds and lakes.

Distribution. Endemic in southern South America. Occurs on suitable bodies of water from Peru, northern Bolivia, Paraguay, and Uruguay to Tierra del Fuego (*P. r. chilensis*; other race, *rolland* confined to Falkland Islands). Occurs throughout the chaco, but only on the relatively few larger bodies of water. The chaco forms the northeastern border of the species' range.

Podiceps major Great Grebe

Taxonomy. Monotypic, not closely related to other species.

Ecology. Diver, requires large bodies of water for nesting. Probably partly migratory.

Distribution. Endemic in southern South America. Distribution uncertain in north because of lack of knowledge of migration. Appears to nest N as far as the fringes of the chaco, perhaps in a few places farther N in the chaco. Occurs from the chaco and central Chile S to Tierra del Fuego.

Podilymbus podiceps Pied-billed Grebe

Taxonomy. Polytypic. Forms a superspecies with isolated Guatemalan *P. gigas*. Known from Pleistocene of Minas Gerais.

Ecology. Swimmer and diver inhabiting small ponds and other bodies of water. Occupies suit-

able ponds and other sites from the central chaco southward. Partly migratory.

Distribution. New World. *Podilymbus podiceps antarcticus* occupies South America N to Panama and S to Tierra del Fuego. It appears not to breed in Amazonia, south-central or northeastern Brazil, southern Peru, or northern Chile. Thus, there is a hiatus between the northern chaco to southeastern Brazil and northern Peru to Venezuela and the Guianas. Occupies all the chaco except the northern edge (northern Paraguay, Santa Cruz, Mato Grosso).

FAMILY PHALACROCORACIDAE

Phalacrocorax olivaceus Olivaceous Cormorant

Taxonomy. Polytypic. Forms superspecies with Nearctic *P. auritus* (Mayr and Short, 1970). Known as a fossil from the Pleistocene of Minas Gerais; a paleospecies, *P. pampeanus*, is known from the Upper Pleistocene of Buenos Aires.

Ecology. Dependent on large, open bodies of water for fishing; nests in trees or on cliffs near water. Nonmigratory. Probably nests in very few places in the chaco, possibly in the northern pantanal and larger bañadas.

Distribution. New World, southern United States to Tierra del Fuego. *Phalacrocorax olivaceus brasiliensis* occurs from Costa Rica to northern Tierra del Fuego, and is weakly differentiated (mainly by larger size) from the race inhabiting the latter island. Occurs throughout the chaco, but rarely breeds.

FAMILY ANHINGIDAE

Anhinga anhinga New World Anhinga

Taxonomy. Polytypic. Comprises a superspecies with *A. rufa* (Ethiopian), *A. melanogaster* (Asia), and *A. novaehollandiae* (Australasia) (Mayr and Short, 1970).

Ecology. Fishes in diverse swamps and ponds in wooded areas. Nonmigratory.

Distribution. New World, mainly tropical and subtropical from southern Nearctic to central Argentina (E of Andes). *Anhinga anhinga anhinga* occurs from Panama S, including major (permanent) streams in eastern chaco, and to N, E, and

SE from there; its southern limit is Buenos Aires (delta of Rio de la Plata).

FAMILY ARDEIDAE

Botaurus pinnatus Pinnated Bittern

Taxonomy. Polytypic. Forms superspecies with *B. lentiginosus* (Nearctic), *B. stellaris*, and *B. poeciloptilus* (last two Old World; Mayr and Short, 1970); probably is nearest to *lentiginosus*.

Ecology. Inhabits marshlands, nests in reeds. Migratory.

Distribution. New World from Mexico discontinuously to central Argentina. *Botaurus pinnatus pinnatus* occurs from Nicaragua to Argentina. The South American population nests in the northern pampas and most of the chaco (except northern Paraguay, Santa Cruz), as well as areas at the base of the Andes to the W, and in Argentine Mesopotamia¹ to the E. Probably nests in northern South America, and east-central Brazil, but migrant in Amazonia.

Ixobrychus involucris Stripe-backed Bittern

Taxonomy. Monotypic. Probably an ancient derivative of ancestral *minutus-exilis* stock.

Ecology. Inhabits marshlands, nests in marsh grasses. Migratory.

Distribution. Endemic in southern South America. Nests in the southern chaco from southern Paraguay S to Río Negro, extending E through eastern Paraguay to Rio de Janeiro, and the Atlantic Coast, SE to Uruguay, SW to central Chile, W to Chile in the S, and to Salta in the N. Perhaps breeds N of this range, but probably is migratory beyond Paraguay.

Tigrisoma lineatum Rufescent Tiger-heron

Taxonomy. Polytypic. Closely related to the broadly sympatric *T. fasciatum*.

Ecology. Inhabits woodland swamps and water courses (even small ones). May be migratory in extreme south.

¹Argentine Mesopotamia is a geographical name for the area between the Uruguay and Parana rivers, including Misiones, Corrientes, and Entre Ríos provinces.

Distribution and variation. New World. Occurs from Middle America to central Argentina, E of the Andes. *Tigrosoma lineatum marmoratum*, one of several races distinct because of size, color markings, and the amount of feathering at the base of the bill, is the southernmost subspecies, occurring throughout the chaco in wet areas that are more densely wooded, and extending beyond the chaco NW to northern Bolivia, N to northern Mato Grosso and Maranhão, NE and E to the Atlantic Coast, S to Rio Grande do Sul, northern Uruguay, northern Buenos Aires, and Córdoba, and W to the foothills of the Andes.

Nycticorax nycticorax
Black-crowned Night Heron

Taxonomy. Polytypic. Forms superspecies with Australasian *caledonicus* (Mayr and Short, 1970).

Ecology. Water-dependent, forages in water usually at night and early morning and evening. Partly migratory. Nests in trees in loose colonies.

Distribution. Found in much of Old World and throughout New World. *Nycticorax nycticorax hoactli* occurs in all of South America (except southern Chile) and northward into Middle America. Found at scattered points throughout the chaco where there is sufficient water.

Pilherodias pileatus
Capped Heron

Taxonomy. Monotypic. No close relatives.

Ecology. Water-dependent, nonmigratory, essentially tropical.

Distribution. Essentially South American, Panama S to Paraguay and southeastern Brazil, E of Andes. Occurs northward and eastward from the central Paraguayan chaco, including Santa Cruz and Mato Grosso.

Syrigma sibilatrix
Whistling Heron

Taxonomy. Polytypic. Relationships uncertain.

Ecology. Water-dependent, but occurs in wet grasslands as well as wetter areas; essentially a savanna and open country heron. Nonmigratory.

Distribution and variation. Endemic in South

America. Widely disjunct populations in the llanos of Colombia and Venezuela, and in the south-central part of the continent from Bolivia to Uruguay. The southern disjunct is racially distinct (*S. sibilatrix sibilatrix*), differing slightly in color and in size from the northern form, and occurring throughout the chaco except in the most arid central portion from western Formosa S to Córdoba, that is, it occurs in the more moist areas. It extends beyond the chaco NW to northern Bolivia, N to southern Mato Grosso, NE to São Paulo, E to the Atlantic Coast, SE to Uruguay, S in the east to northern Buenos Aires and in the west to Tucumán, and W to the lower Andean slopes.

Butorides striatus
Striated Heron

Taxonomy. Polytypic. Comprises a superspecies with the generally shorter billed and more rufescent North and Middle American *virescens* (*sundevalli* of the Galapagos may be specifically distinct from *striatus*, and part of this superspecies). Appears to hybridize with *virescens* in Panama, but extent of interbreeding is unknown.

Ecology. Inhabits wooded swamps, small streams, ponds, and mangroves. May be partly migratory in extreme south.

Distribution and variation. Nearly cosmopolitan, if Old World forms are indeed conspecific; the superspecies may have originated in the New World. In South America *striatus* occurs from Panama to Peru in the W, and to southern Buenos Aires in the E. *Butorides striatus fuscicollis* inhabits wet areas throughout the chaco, which forms the northwestern portion of its range. It extends E to São Paulo and the Atlantic Coast, S to La Pampa and Buenos Aires, and W into the lower Andean foothills. The races are moderately distinct, *fuscicollis* being distinguished mainly by its pale coloration.

Egretta thula
Snowy Egret

Taxonomy. Polytypic. Forms a superspecies with Old World *E. garzetta* (Mayr and Short, 1970).

Ecology. Wanders after breeding. Partly

migratory. Marshes, swamps, colonial nesting habits.

Distribution. New World. *Egretta thula thula* occurs throughout much of South America and into Middle America. Its southern limits are central Chile and southern Buenos Aires Province. Occurs throughout the chaco and beyond in all directions, but very restricted within the chaco during the breeding season, when it probably is confined to the eastern and northern swampy areas.

Egretta alba
Great Egret

Taxonomy. Polytypic. No very close relatives. Known as a fossil from the Pleistocene of Venezuela.

Ecology. Post-breeding wanderer. Partly migratory. Inhabits all types of wet areas—grasslands, marshes, swamps—but nests colonially in trees.

Distribution. Nearly cosmopolitan in warmer areas. *Egretta alba egretta* inhabits the New World, occurring in South America S to south-central Chile and Patagonia.

Ardea cocoi
White-necked Heron

Taxonomy. Monotypic. *Ardea cocoi*, *A. cinerea* of Middle and North America and Eurasia, *A. melanocephala* of Africa, and possibly Australian *A. pacifica* form a superspecies. Pleistocene fossil material of *cocoi* is known from Venezuela.

Ecology. Partly migratory, frequents all types of wet areas, but nests colonially in trees.

Distribution. Essentially South American (to Panama), occurring S to south-central Chile and northern Patagonia. Found in wetter parts of the chaco.

FAMILY CICONIIDAE

Mycteria americana
Wood Stork

Taxonomy. Monotypic. Kahl (1971) considered the Wood Stork related closely to tropical Old World species (e.g., *cinereus*) of the genus *Ibis*, hence merged in *Mycteria*.

Ecology. Frequents swamps, marshes, and wet areas. Wanders or migratory in extreme south. Nests colonially in trees.

Distribution. From the southern fringe of the Nearctic to Peru in western South America and Buenos Aires in eastern South America. Occurs throughout the chaco, but breeding restricted to the moist areas in the E and W. Extends beyond chaco to N, E, and S.

Ciconia maguari
Maguari Stork

Taxonomy. Monotypic. Merged in the genus *Ciconia* by Kahl (1971), and is the only extant species of that genus in the New World. Known as a fossil from prehistoric sites in Santiago del Estero, *Ciconia maltha* was a widely distributed Pleistocene stork in the Nearctic, and *Prociconia (Ciconia?) lydekkeri* is known from Upper Pleistocene deposits in Minas Gerais.

Ecology. Partly migratory (extreme S) occurring in wet grasslands as well as marshes and swamps. Found in flooded fields, sometimes in dry fields away from wet areas.

Distribution. Endemic in South America, ranging E of the Andes from Colombia and Venezuela to Río Negro, Argentina, but not in the upper Amazon Basin (Colombia to Bolivia). Occurs throughout the chaco; widespread during summer rains in open areas, otherwise frequents wetter eastern and western portions of the chaco. Extends beyond the chaco to the N, E, and S.

Jabiru mycteria
Jabiru

Taxonomy. Monotypic. No close relatives.

Ecology. Favors marshes and swamps in partly or lightly wooded country. Post-breeding wanderer. Nests in woodlands, not necessarily in wet areas, and not in colonies.

Distribution. Discontinuously distributed (gap S of Amazon) from northern Middle America to Tucumán and Uruguay. Common in the pantanal and adjacent moist eastern chaco, and also in the southwestern fringes (Tucumán) of the chaco; only of sporadic occurrence in the south-central chaco and not known in the northern Paraguayan and Bolivian portions (however,

probably occurs in such wet areas as the Bañados del Izozog in southwestern Santa Cruz).

FAMILY THRESKIORNITHIDAE

Plegadis chihi

White-faced Glossy Ibis

Figure 18

Taxonomy. Monotypic. Comprises a super-species with Nearctic and Old World *P. falcinellus* (Mayr and Short, 1970). Andean *P. ridgwayi* probably represents an early derivative of an ancestor in common with *chihi-falcinellus*.

Ecology. Open swamps, marshes, and wet grasslands; not a forest ibis. Nests colonially in

trees. A post-breeding wanderer, perhaps migratory in south.

Distribution. Discontinuously distributed in the western and southern Neartic, Middle America, northern South America (Mato Grosso, São Paulo, S to Río Negro, Argentina, and W to central Chile). Status uncertain in coastal Peru. A hiatus exists between Venezuela and eastern Bolivia. Occurs in suitably wet areas of the chaco, and extends (as part of the southern disjunct group of populations) E to São Paulo and the Atlantic Coast, and S and SW to the limits of the species' range. *Plegadis falcinellus* seems to be extending its range, and now breeds in coastal Venezuela (P. Schwartz, *vide* E. Eisenmann).

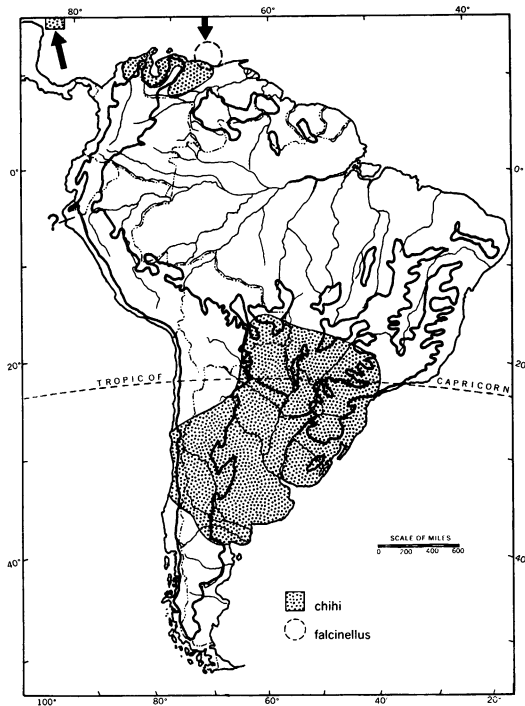


FIG. 18. Range of White-faced Glossy Ibis (*Plegadis chihi*). Disjunct populations of this monotypic species occur to North America, as indicated by left arrow. Broad disjunction occurs within South America, as shown. *Plegadis chihi* forms a superspecies with *P. falcinellus*, which occurs in North America and the West Indies, and seems to be invading coastal Venezuela (right arrow). Distribution of *chihi*: wet areas, usually in open country, and especially in semiarid zones.

Harpiprion caerulecens

Plumbeous Ibis

Taxonomy. Monotypic genus and species. No close relatives.

Habitat. Marshy and swampy areas. Little known.

Distribution. Endemic in south-central South America. The chaco forms the southwestern part of the species' range that extends N to central Mato Grosso, E to eastern Paraguay and coastal Rio Grande do Sul, SE to northern Uruguay, S to Córdoba and Entre Ríos, and W just beyond the chaco into subtropical forests of the Andean foothills (central Bolivia to Tucumán).

Theristicus caudatus

Buff-necked Ibis

Taxonomy. Monotypic genus and species. A lowland form (*caudatus*) has been considered specifically distinct from the disjunct highland group (*melanopsis*) of races.

Ecology. Nonmigratory. Frequents savannas, swamps, marshes, and even dry woodlands (Patagonia). Colonial. Forages in water while wading.

Distribution and variation. Endemic in South America. Lowland *caudatus* occurs from northern Colombia and coastal Venezuela S to Buenos Aires, with a hiatus in southeastern Venezuela; it does not occur in northwestern Brazil, southeastern Colombia, most of lowland eastern Peru, and northern Bolivia. This form inhabits the entire chaco except westernmost Paraguay and adjacent Bolivia; it extends beyond the chaco to the N, E to the Atlantic Coast, S to Córdoba,

Buenos Aires, and Uruguay, and W to the fringes of the subtropical Andean forest in Argentina, and in Santa Cruz, Bolivia. The highland *melanopsis* group occurs from the puna of Ecuador S to Tierra del Fuego, extending to coastal Peru and Chile, and into the Patagonian lowlands of Argentina. The two groups are disjunct, and they differ in color pattern; *caudatus* has a black breast and belly, whereas the *melanopsis* group has a pale breast and more cinnamon in the head and crest.

Phimosus infuscatus
Bare-faced Ibis

Taxonomy. Monotypic genus and species. No close relatives.

Ecology. Swampy and marsh areas (esteros) are favored by this ibis. Scarce everywhere.

Distribution and variation. Endemic in South America. Discontinuously distributed, with disjunct northern South American, and south-central South American populations. The northern form occurs from northern Colombia E to Surinam and S only to the northern edge of Brazil. There is an Amazonian hiatus, south of which occur populations assigned to two races. These populations include a northeastern campo form extending from Maranhão through campos and the Brazilian highlands SW to western Mato Grosso and Paraguay, and *P. i. infuscatus* which occurs from Beni, Bolivia, S throughout the chaco and beyond it E to the Mato Grosso border, eastern Paraguay, Misiones, and Uruguay, S to northern Buenos Aires and Córdoba, and W to the lower Andean slopes. *Phimosus infuscatus infuscatus* is smaller and shorter-billed than the contiguous race *nudifrons*, and these differ from northern South American populations in size, bill size, and color of the facial area.

Platalea ajaja
Roseate Spoonbill

Taxonomy. Monotypic. The sole member of its genus in the New World, merged in *Platalea* by Mayr and Short, 1970.

Ecology. Marshy areas, lagoons, lakes. Nests colonially. Wanders after breeding. Wades while foraging, straining out food with spatulate bill.

Distribution. Occurs from southern Nearctic through Middle America S to the chaco and

southern Brazil, and sparingly beyond to northern Buenos Aires and Uruguay.

FAMILY ANHIMIDAE

Chauna torquata
Southern Screamer
Figure 19

Taxonomy. Monotypic. Forms superspecies with *C. chavaria* of northeastern Colombia and northwestern Venezuela. Differs from *chavaria* in larger size, markings on breast, different banding of neck, and lack of white on head.

Ecology. Marshes, esteros, pantanal, flooded pampas. Occurs in pairs or small groups. Forages while wading. Nonmigratory.

Distribution. Occurs in wetter, open areas of the chaco, and beyond N to the savannas of Beni,

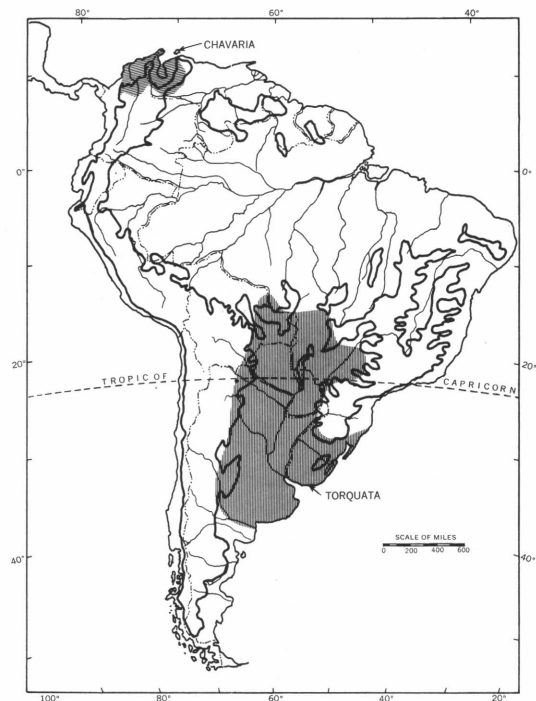


FIG. 19. Range of Southern Screamer (*Chauna torquata*) and its disjunct northern allo-species *C. chavaria*. Distribution of *torquata* is pampas-chaco-campo, but it is essentially a pampas species that occurs in wet areas of adjacent regions; it does not occupy entire campo region.

Bolivia, and to central Mato Grosso, E to São Paulo, Misiones and coastal Rio Grande do Sul, S to Rio Negro, and W to the base of the Andes.

FAMILY ANATIDAE

Dendrocygna bicolor
Fulvous Whistling Duck

Taxonomy. Monotypic. Forms a superspecies with Asian *D. arcuata* (Mayr and Short, 1970).

Ecology. Esteros, lagoons, swamps, lakes in pampas, campos, and the chaco. Forages while swimming and on land. Nonmigratory.

Distribution. New World. Discontinuously distributed through Middle America, in northern South America, and S of the Amazon. A hiatus exists in Amazonia. The southern disjunct population occurs throughout the campo region from Maranhão S through Mato Grosso and eastern and central Paraguay to Córdoba, southern Buenos Aires, Uruguay, and Rio Grande do Sul. It inhabits most of the chaco in favorable situations, except in far western Paraguay and Bolivia.

Dendrocygna viduata
White-faced Whistling Duck

Taxonomy. Monotypic. No very close relative in its genus.

Ecology. All manner of wet areas in forests and open country. Nonmigratory.

Distribution. Tropical Old World as well as New World. More continuously distributed in South America than is *D. bicolor*, occurring throughout the lowlands from northern Colombia E and S to Tucumán and southern Buenos Aires, Argentina, including the entire chaco in suitable habitats.

Dendrocygna autumnalis
Black-bellied Whistling Duck

Taxonomy. Polytypic. Appears related to the largely allopatric West Indian *D. arborea*.

Ecology. Marshes, swamps, flooded grasslands. Requires trees for nesting. Not known to be migratory.

Distribution. Neotropics, from Texas to South America. *Dendrocygna autumnalis autumnalis* occurs throughout the South American

range of this species, including the northern chaco (Paraguay, Bolivia) and perhaps the western fringes of the southern chaco (Argentina). It is uncertain whether there is a hiatus across northern Amazonia, and the status of the species in western Peru is uncertain. Otherwise extends from the northern chaco W into the lower Andes (S from there to Tucumán), N to the Amazon River, and E to the Atlantic Coast (S along it to Rio Grande do Sul).

Neochen jubata
Orinoco Goose

Taxonomy. Monotypic species and genus. Related closely to *Chloephaga*, *Alopochen* (Africa), and to the extinct genus *Anabernicula* (see Short, 1970) known thus far only from the Nearctic. Two paleospecies of *Neochen* are known from the Upper Pleistocene of Argentina and Brazil (Brodkorb, 1964).

Ecology. A little-known species inhabiting wooded swamps and lagoons. Nonmigratory.

Distribution. Endemic in South America, occurring E of the Andes from central and eastern Venezuela S to northwestern Argentina, the northern Paraguayan chaco, and Mato Grosso, and E to Maranhão and Goiás. Found in the wet areas of the pantanal in Mato Grosso, in the Bolivian chaco, and in a few places (perhaps far-eastern and far-western only) in the northern Paraguayan chaco and possibly in the fringe of the chaco in Salta.

Cairina moschata
Muscovy Duck

Taxonomy. Monotypic species. Related *C. scutulata* occurs in Southeast Asia.

Ecology. Inhabits chiefly wooded swamps, forest streams, and lagoons, but also occurs to some extent in marshes. Nonmigratory.

Distribution. New World tropics, essentially continuously distributed from Mexico to northern Argentina and Uruguay. Occurs sporadically throughout the chaco, usually in wetter places and especially in the eastern and western edges. The chaco essentially forms the southwestern border of the species' range, although it reaches the Andean foothills in the W.

Sarkidiornis melanotos
Comb Duck

Taxonomy. Monotypic genus, polytypic species. One subspecies in South America, another in the Old World tropics. One paleospecies known from the Quaternary of Mauritius (Brodkorb, 1964), and *S. melanotos* is reported from the Pleistocene in Buenos Aires.

Ecology. Found in diverse wet areas—marshes, lagoons, flooded grasslands, forest streams. Nonmigratory.

Distribution. Pan-tropical, *Sarkidiornis melanotos sylvicola* occurs from Panama discontinuously S to northwestern Peru W of the Andes, and to the southern chaco, Entre Ríos, and Uruguay E of the Andes. Gaps in distribution occur in western and northern Amazonia, with the southeastern disjunct population ranging S from the lower Amazon River. The southwestern limit of this population occurs along the southern and western border of the chaco. Locally common in the wetter eastern and western chaco, sporadic in the central portion, and apparently absent from northwestern Paraguay and from the Bolivian chaco. Extends beyond the chaco slightly to the S (Córdoba, southern Santa Fe), E to the Uruguay River and Misiones, and NE to the lower Amazon Valley, Ceará, Bahía, and Rio de Janeiro.

Callonetta leucophrys
Ringed Teal

Taxonomy. Monotypic genus and species. No close relatives.

Ecology. Found in esteros and marshes of the southern chaco and northern pampas. Migrates northward and eastward for the winter (Olog, 1963).

Distribution. Endemic in northern Argentina, occurring from Santiago del Estero and Chaco S to Tucumán, Entre Ríos, and northern Buenos Aires. Possibly breeds somewhat farther N sporadically.

Amazonetta brasiliensis
Brazilian Duck

Taxonomy. Monotypic genus and species. No close relatives. Fossil material of this species is

reported from the Pleistocene of Minas Gerais, Brazil (Brodkorb, 1964).

Ecology. Frequents lowland wet areas of all types, both in forested and open regions. Not known to be migratory.

Distribution and variation. Endemic in South America, occurring from northern Colombia S in the lowlands E of the Andes to eastern and southern Brazil, Uruguay, Buenos Aires, and Córdoba. A southern race, *ipecutiri*, distinguished by larger size from the nominate form, occurs at suitable sites throughout the chaco except in extreme northern Paraguay, Bolivia, and Mato Grosso, where it is replaced by the nominate race. The species extends slightly S beyond the chaco to Córdoba and Buenos Aires, and, of course E and N from the chaco.

Anas versicolor
Silver Teal

Taxonomy. Polytypic, one of several species of South American *Anas*.

Ecology. Lakes, ponds, marshes, flooded grasslands, generally in open country. Partly migratory.

Distribution and variation. Endemic in South America, essentially in temperate zone of central Andes (Peru to Jujuy, Argentina), and lowlands from southern edge of Chaco and Rio Grande do Sul S to Tierra del Fuego. Three races are recognized, including the small and dark *versicolor*, which reaches the southern edge of the chaco from farther S (extends S to northern Patagonia, W to central Chile). This race and the contiguous population from southern Patagonia have been treated as specifically distinct from the Andean *A. v. puna* (but see Johnsgard, 1965).

Netta peposaca
Rosy-billed Pochard

Taxonomy. A monotypic species, not related very closely to other species of *Netta*.

Ecology. Favors lakes and marshes in more or less open terrain. Partly migratory.

Distribution. Endemic in South America, chiefly temperate zone from southern chaco, Rio Grande do Sul and central Chile S to the fringes of Patagonia, and with a disjunct population in

Tierra del Fuego. Breeds along the southern edge of the chaco (Tucumán, Santiago del Estero, Santa Fe), and to the S. May breed N into the central chaco sporadically. The southern edge of the chaco is marked by large esteros (e.g., northwestern Santa Fe) mixed with intrusions of pampas vegetation and chaco woodland.

Heteronetta atricapilla
Black-headed Duck

Taxonomy. Monotypic genus and species.

Ecology. Found in diverse marshes, swamps, esteros, but centered in pampas. Partly migratory. Is a nest parasite on other waterbirds.

Distribution. Endemic in southern South America. Occurs in the more moist eastern chaco from southern Paraguay (northern limit of its range) S and E to Rio Grande do Sul, Uruguay, and northern Río Negro, and to the W south of the chaco as far as the central Chilean coast.

Oxyura dominica
Masked Duck

Taxonomy. Monotypic species, distinct within *Oxyura*. Known as a fossil from the Pleistocene of Minas Gerais (Brodkorb, 1964).

Ecology. Found in diverse watery situations (ponds, lagoons, swamps, lakes, esteros). Nonmigratory, less flock-forming tendency than other ducks.

Distribution. Neotropics from Texas to Argentina, occurring S to Peru W of the Andes, and E of them S (except northern Bolivia) to Córdoba and Buenos Aires, Argentina, and Uruguay. Found throughout the chaco in favorable situations, except in the northwest (Bolivian chaco), and occurring slightly beyond it to the W and S.

Oxyura vittata
Lake Duck

Taxonomy. Monotypic. A close relative of *O. jamaicensis*, with which it is partly sympatric.

Ecology. Open water, chiefly in lakes, marshes, and esteros in open country. Partly migratory.

Distribution. Endemic to southern South America. Occurs from southern edge of chaco as well as central Chile and Rio Grande do Sul S to

Tierra del Fuego. Inhabits chiefly the wet southeastern chaco (Santiago del Estero to Corrientes) along the fringe of the pampas, and southward from there.

FAMILY CATHARTIDAE

Cathartes aura
Turkey Vulture

Taxonomy. Polytypic. Closely related to *C. burrovianus*. Known from the Pleistocene of Buenos Aires and Minas Gerais (Brodkorb, 1964).

Ecology. Woodlands, open country, arid lands. A scavenger, flocking to feed on carrion, to migrate, to roost.

Distribution and variation. Widespread Nearctic to Tierra del Fuego. Breeds at least sporadically throughout South America, except coastal Argentina and probably the western and central chaco. *Cathartes aura ruficollis*, blacker (less brown) than the other races and with the head banded with yellow, occurs from Panama through northern Colombia and lowland areas E of the Andes S to western Paraguay, Santa Fe, northern Buenos Aires, and Uruguay. It occurs in the northern chaco, and the eastern chaco, and to the N, E, and SE. It is uncertain whether this race sporadically breeds across the western chaco; likewise it is unknown whether the Andean race reaches the western fringe of the chaco, or whether it meets *ruficollis* in the chaco region.

Cathartes burrovianus
Lesser Yellow-headed Vulture

Taxonomy. Monotypic. Closely related to sympatric *C. aura*.

Ecology. A scavenger occupying diverse habitats largely within the tropics.

Distribution. Neotropics; Middle America through the lowlands of South America E of the Andes, S to Uruguay and northeastern Argentina (missing from parts of Venezuela, the Guianas, and adjacent Brazil). Within the chaco it is confined to the moist eastern fringe, mainly along the Paraguay River S to Corrientes and Chaco provinces. Extends N, E, and SE from that part of the chaco.

Coragyps atratus
Black Vulture

Taxonomy. Monotypic genus, polytypic species. Known from the Pleistocene of Minas Gerais.

Ecology. A scavenger, flocking more than species of *Cathartes*, and found in all kinds of habitats.

Distribution. North America S to fringes of Patagonia, *C. a. brasiliensis* occurring from Mexico to the southern limit of the species' range. Found throughout the chaco and beyond it in all directions (S to Buenos Aires, Neuquén, central Chile).

Sarcoramphus papa
King Vulture

Taxonomy. Monotypic genus and species. Known from the Pleistocene of Minas Gerais (Brodkorb, 1964).

Ecology. A large, mainly solitary scavenger of wooded regions.

Distribution. Mainly tropical in Middle America and South America S to the southern fringe of the chaco. Sporadically inhabits all but the southeastern edge of the chaco, but nesting possibly confined to the eastern moist region (breeding uncertain S of Paraguay), and to the western fringes (perhaps nesting only in subtropical forests along Andean foothills). At any rate it is uncommon to rare in the Argentine chaco. Its chaco range forms the southernmost extent of the range of the species; from the chaco it extends N through South America and E through eastern Paraguay to Rio de Janeiro.

FAMILY ACCIPITRIDAE

Leptodon cayanensis
Gray-headed Kite

Taxonomy. Monotypic genus and species.

Ecology. Lowland tropical and subtropical woodlands, especially in vicinity of streams.

Distribution. Neotropics, Middle America to Chaco Province, Argentina, and Rio Grande do Sul. Occurs in the northeastern chaco, chiefly in the vicinity of the Paraguay River, from Santa Cruz, Bolivia, S to northeastern Chaco and north-

ern Corrientes. This portion of the chaco forms the southwestern border of the species range; from there it extends E to the Atlantic Coast, and N and NW throughout Amazonia and to the N of there.

Chondrohierax uncinatus
Hook-billed Kite

Taxonomy. Monotypic genus, polytypic species. Known from Pleistocene deposits in Minas Gerais (Brodkorb, 1964).

Ecology. A woodland kite favoring wet areas, feeding on snails and to some extent on other aquatic animals.

Distribution. Neotropical, from Texas and West Indies to northern Argentina. *Chondrohierax uncinatus uncinatus* occurs from Mexico S to Peru in the W, and to Tucumán and Corrientes E of the Andes. Occurs chiefly in the wetter northeastern and western parts of the chaco, and not recorded from the central chaco region of Argentina. The portion of the chaco that *uncinatus* inhabits constitutes the southern extreme of its range; it extends NW along the edge of the Andes, N throughout Amazonia, and E through eastern Paraguay and Misiones to Rio de Janeiro.

Elanoides forficatus
Swallow-tailed Kite

Taxonomy. Monotypic genus, polytypic species.

Ecology. Inhabits wet woodlands and savanna. Migratory in part.

Distribution. New World. Occurs from southern United States S to Argentina; *E. f. yetapa*, the southern race, breeds from Guatemala to northern Colombia, and, E of the Andes, through lowlands and hilly country to the central chaco region, Misiones, and Rio Grande do Sul. Distribution complicated by migration and by dispersal beyond breeding range (wandering birds). Probably breeds in the extreme western chaco (and adjacent subtropical forests from Salta and Jujuy N), in the eastern chaco (vicinity of Paraguay River in Paraguay and possibly Formosa), and perhaps in scattered wetter spots in the northern chaco (Santa Cruz, northern Paraguay).

Gampsonyx swainsonii
Pearl Kite

Taxonomy. Monotypic genus, polytypic species.

Ecology. Favors open and semi-open country, including dry regions.

Distribution and variation. New World. Discontinuously distributed from Middle America S to Peru in the W, and in more or less open areas E of the Andes through the Guianas to the lower Amazon, and thence S to eastern Bolivia, most of the chaco, and São Paulo. *Gampsonyx swainsonii swainsonii* is the race inhabiting the chaco from Tucumán and chaco N, and beyond to northern Bolivia, eastern Paraguay, and eastern Brazil N as far as the Amazon River. This race differs from the other two in lacking rufous coloring on its sides.

Elanus leucurus
White-tailed Kite

Taxonomy. Polytypic. Comprises a superspecies with *E. caeruleus* (much of Old World) and *E. notatus* (Australia; Mayr and Short, 1970).

Ecology. Rather strictly a savanna, grassland, and woodland edge species. Nonmigratory, but irregular post-breeding movements are known.

Distribution and variation. New World, discontinuously distributed from the United States to Patagonia. *Elanus leucurus leucurus* occupies the South American portion of the species' range, inhabiting: part of the Magdalena Valley in Colombia; the llanos region of Venezuela and Colombia, also the Guianas; and, separated by a great hiatus in Amazonia and the campos region of Brazil, southern Brazil to Patagonia. This race occurs in the southeastern chaco (eastern Paraguayan chaco southward), mainly in the pantanal and the chaco-pampas ecotone. It extends beyond E to Rio de Janeiro, and S to central Chile, Río Negro and Chubut, and Uruguay.

Rostrhamus sociabilis
Snail Kite

Taxonomy. Polytypic species. Closely related to *R. hamatus*.

Ecology. Dependent upon snails obtained at edge of water in savannas, grasslands, forests. Partly migratory.

Distribution. New World, southern Florida to Buenos Aires. *Rostrhamus sociabilis sociabilis* inhabits southern Middle America, and South America W to the Andes to Ecuador, and throughout the lowlands E of the Andes to Tucumán, Córdoba, Buenos Aires, and Uruguay. Occurs throughout the chaco, but mainly in the wetter eastern and western parts.

?*Harpagus diodon*
Rufous-thighed Kite

Taxonomy. Monotypic species, related to sympatric *H. bidentatus*.

Ecology. Inhabits forest; not well known.

Distribution. Endemic in South America, discontinuously distributed in the lower Amazon region, and S of the Brazilian campos in forested southeastern Brazil from Bahia to eastern Paraguay, Misiones, and Rio Grande do Sul. Occurs also in Jujuy and Salta, Argentina, but its status in these provinces is uncertain; this latter range is within subtropical forest but at its border with western fringes of the chaco, hence its questionable status as a chaco species.

Ictinia plumbea
Plumbeous Kite

Taxonomy. Monotypic. Forms superspecies with the North American *I. mississippiensis* (Mayr and Short, 1970), with which it has been merged (Sutton, 1944).

Ecology. A woodland and forest kite especially frequenting riparian areas. Partly migratory. Largely insectivorous.

Distribution. New World, from Middle America more or less continuously S to Ecuador in the W, and, E of the Andes in areas S to the southern chaco, Corrientes, and Rio Grande do Sul. Found throughout the chaco in wet areas, and denser groves of trees. Extends beyond the chaco W into subtropical forest, E to Misiones, eastern Paraguay and the Atlantic Coast of Brazil, and of course to the N.

Geranospiza caerulescens
Crane Hawk

Taxonomy. Monotypic genus, polytypic species.

Ecology. Favors wooded areas near water,

swamps, riverine situations, wet areas in dry country.

Distribution and variation. Neotropics from Middle America more or less continuously to western Peru, and in the E through lowland South America (except northern Bolivia) to the southern chaco and Uruguay. *Geranospiza caeruleascens flexipes* occurs in wet situations throughout the chaco, but especially in the more moist eastern and western chaco; it extends beyond the chaco W into the subtropical deciduous forest, N to northern Mato Grosso and Goiás, and E across Paraguay and southeastern Brazil to the Atlantic Coast. This race is larger and paler than the more northern, adjacent *gracilis*. The *gracilis* group once was considered specifically distinct from the northern South American *caeruleascens* group, and from the Middle American and northwestern South American *nigra* group.

Circus buffoni

Long-winged Harrier

Taxonomy. Monotypic species. Not closely related to other congeneric harriers.

Ecology. Frequents open country usually near water—marshlands, grasslands, savannas. Nests in grass or reeds. Migratory.

Distribution. Endemic in South America, with widely disjunct, undifferentiated populations in the Guianas and Venezuela, and from Mato Grosso and São Paulo to southern Buenos Aires and perhaps beyond. Status uncertain in Patagonia, Chile, and northern fringes of its range in southern South America, both because of migration, and post-breeding wandering. Breeds in the eastern chaco, especially in the pantanal and the southern (pampas-chaco ecotone) fringes.

Accipiter bicolor

Bicolored Hawk

Taxonomy. Polytypic. It forms superspecies with *A. cooperii* of North America and *A. gundlachi* of Cuba (Mayr and Short, 1970).

Ecology. A hawk of the edges of woodlands, where it feeds mostly on birds.

Distribution and variation. Middle America and South America. Discontinuously distributed in South America, S to Peru in the W, and to the southern chaco and Rio Grande do Sul in the E; also occupies most of Chile and adjacent Argentin-

ina. A less streaked, more rufous race *guttifer* occupies the chaco, except for the dry central chaco of Argentina. This race extends beyond the chaco N to northern Bolivia and central Mato Grosso, and E to eastern Paraguay and Corrientes (intergrading to the N and E with adjacent forms). *Accipiter bicolor guttifer* occupies the southern edge of the continuous range of this species, without contact with the Chilean population.

Accipiter striatus

Sharp-shinned Hawk

Taxonomy. Strongly polytypic, forming a superspecies with Old World *A. nisus* (also *rufiventris*, *madagascariensis*; see Mayr and Short, 1970).

Ecology. Wooded and semiwooded areas; spottily distributed even in favorable habitat. Partly migratory. Feeds mainly on small birds.

Distribution and variation. New World, discontinuously distributed from Canada to Argentina. Various forms have been considered specifically distinct, including an Andean form, and a lowland South American population. The latter, *A. s. erythrocnemius* occurs in all but the northern chaco (northern Paraguay, Santa Cruz), in the subtropical Andean slope forests of Argentina W of the chaco, in the chaco-pampas ecotone to the S, E to Uruguay and São Paulo, and NE to Mato Grosso and Bahia. The northern Andean form, *A. s. ventralis*, apparently does not meet *erythrocnemius* in Bolivia. *Accipiter striatus erythrocnemius* differs from *ventralis* in its lesser individual variation, less frequent color phases, and more barred underparts (Brown and Amadon, 1968).

Buteogallus urubitinga

Great Black Hawk

Taxonomy. Polytypic. Rather closely related to the *anthracinus-aequinoctialis* superspecies.

Ecology. Found in trees near water in savannas, forests, and arid scrub.

Distribution and variation. Middle America and South America. Occurs S to Peru, and, E of the Andes, S to Tucumán, Entre Ríos and Uruguay. *Buteogallus urubitinga urubitinga* occupies the South American part of the range, and inhabits the entire chaco, although rare in the central

chaco and of only sporadic occurrence in the southern fringes of the chaco. Extends W of the chaco into subtropical forest along the Andes, N through Amazonia, E to the Atlantic Coast, and SE barely beyond the chaco to southern Santa Fe and Uruguay.

Harpyhaliaetus coronatus
Crowned Eagle

Taxonomy. Monotypic. Comprises a super-species with montane Middle American and Andean *solitarius*.

Ecology. A woodland and forest eagle, also frequenting edges and open, brushy country. Wide-ranging.

Distribution. Endemic in South America, from the campo region of Mato Grosso and Goiás S (inland from coast) through the chaco, western pampas, and Andean foothills to northern Patagonia. Breeds sparingly throughout the chaco and beyond in all directions. Its smaller, darker, less crested relative *solitarius* is allopatric (Andes to Peru, and, recently reported from northwestern Argentina, *vide* Amadon).

Heterospizias meridionalis
Savanna Hawk

Taxonomy. Monotypic genus and species.

Ecology. Favors marshes and wet savannas such as the pantanal, but occurs in grassland, brushland, forest clearings as well. It is somewhat odd that it does not inhabit the pampas. Nests in trees including planted eucalypts. Frequenting cultivated areas in some regions where forests have been removed.

Distribution. Essentially South American, ranging from Panama to Peru in the W, and to the southern chaco and Uruguay in the E. Occurs throughout the chaco in more open, damp areas, especially in the pantanal. Extends sporadically S of the chaco (pampas-chaco ecotone), and W (to Andean foothills), N, and E from it.

Busarellus nigricollis
Black-collared Hawk

Taxonomy. Monotypic genus, polytypic species.

Ecology. Frequenting water: swamps, ponds, flooded lowlands, pantanal. Preys upon fishes and other aquatic animals.

Distribution and variation. Neotropical, Middle America to southern chaco. Occurs throughout lowland eastern South America (except northern Bolivia) S to Rio de Janeiro, São Paulo, Corrientes, and Tucumán. The larger, whiter-headed southern race *leucocephalus* occurs in wet areas throughout the chaco, and beyond it W to the subtropical foothills of the Andes, N to the chaco edge and southern Mato Grosso, and E to eastern Paraguay and eastern Corrientes.

Geranoaetus melanoleucus
Black-chested Eagle-buzzard

Taxonomy. Polytypic; genus monotypic, relationships unclear. Known from the Pleistocene of Minas Gerais; reported (Brodkorb, 1964) North American and Cuban fossil material needs re-examination.

Ecology. Inhabits primarily rough terrain, mixed woodland, and open country, but also frequents forest areas.

Distribution and variation. Endemic in South America. Occurs along entire Andes chain and E through Patagonia to the arid western pampas and western chaco (race *australis*), and, E from the eastern chaco to Uruguay and Rio de Janeiro (*G. m. melanoleucus*). It is uncertain whether the races intergrade in the central chaco, or the birds there are too sparse to show such effects. At any rate, one race or the other occurs in all parts of the chaco. Eastern *melanoleucus* is weakly differentiated from *australis* by the lack of fine barring on the posterior underparts (Brown and Amadon, 1968).

Parabuteo unicinctus
Bay-winged Hawk

Taxonomy. Monotypic genus, polytypic species.

Ecology. Favors brushlands, woodlands, and forest edges, including xeric habitats. Partly migratory. Preys upon various small animals.

Distribution and variation. Discontinuously distributed from southern Nearctic to central Chile and northern Patagonia, not occurring in Amazonia. In South America occurs along the Andes, in northern Venezuela and Surinam, and (*P. u. unicinctus*) from northwestern Peru discontinuously to central Chile W of the Andes, and E of the Andes from parts of the Marañón Valley and Urubamba Valley, and northern Bolivia E

through the campos and caatinga to Ceará, SE to Rio de Janeiro, and S to western Uruguay, western Buenos Aires and northern Río Negro. This race (*unicinctus*) inhabits the entire chaco (and chaco-scrub zone to S of chaco), albeit sporadically, and beyond it in all directions except SE. Its status in certain parts of this range may be as a migrant.

Buteo nitidus

Gray Hawk

Taxonomy. Polytypic species, of uncertain relationship within its genus (see Mayr and Short, 1970).

Ecology. Inhabits riparian woodlands or groves in less mesic areas, and woodland edges generally, preying mainly upon lizards and snakes (Brown and Amadon, 1968).

Distribution and variation. New World from United States to northern Argentina. Occurs in South America S to Ecuador in the W, and in the E it ranges throughout the lowlands except for the northeastern corner of Brazil, S to Rio de Janeiro, São Paulo, and the chaco to Tucumán and Chaco provinces. *Buteo nitidus pallidus* is a pale almost whitish, moderately distinct subspecies occupying the southern part of the species' range from the Amazon River southward. It inhabits the chaco, favoring the more moist eastern (S to Chaco) and western (S to Tucumán, but apparently not present in northwestern Paraguay and adjacent Bolivia) part of the chaco. Apparently it is absent from the dry central chaco of Argentina. The chaco range forms the southern extreme part of the range of the species, and it extends only to the N from the chaco.

Buteo magnirostris

Roadside Hawk

Taxonomy. Polytypic, no very close relatives in *Buteo*.

Ecology. Occupies diverse habitats, but usually not extensive, dense forests. Feeds mainly on invertebrates, especially insects.

Distribution and variation. New World, common often abundant from Nearctic fringe to northern Argentina, and W of the Andes to Peru. *Buteo magnirostris pucherani* occurs throughout the chaco W of the Paraguay-Parana rivers, SW to La Rioja, and in the E to Santa Fe. This race

extends beyond the chaco W into the forests of the lower Andean slopes, and N and NW through lowland Bolivia to Peru. It is nearest the more eastern *saturatus*, but is larger (largest race of *B. magnirostris*) with narrower, paler breast bars (Brown and Amadon, 1968). *Buteo magnirostris saturatus* occupies the eastern chaco of Corrientes and northwestern Entre Ríos, as well as eastern Paraguay, Rio Grande do Sul, and northern Uruguay. This large form is rufous below, and its head is very dark.

Buteo leucorrhous

White-rumped Hawk

Taxonomy. Monotypic. Relations with other species of *Buteo* have not been established fully.

Ecology. Little known, but apparently a forest and forest-edge species. Nonmigratory, or possibly migratory in the extreme south.

Distribution. Endemic in South America, where it is discontinuously distributed. A group of populations occupies the northwestern part of the continent from northwestern Peru N through Colombia, western Venezuela, and S in eastern Colombia and eastern Ecuador. There is a hiatus to the S, a disjunct population occurring in the subtropical Andean slope forests of northwestern Argentina (perhaps reaching the fringes of the chaco), and another ranging more broadly from the southeastern chaco (eastern Chaco, eastern Formosa) through eastern Paraguay and northern Corrientes to the Atlantic Coast from Rio de Janeiro S to Rio Grande do Sul. The eastern Chaco population occurs in the pantanal, mainly in riverine timber.

?*Buteo brachyurus*

Short-tailed Hawk

Taxonomy. Polytypic, not very closely related to any particular species of *Buteo*. Two major groups, possibly specifically distinct, are the Andean *albigula*, and the lowland *brachyurus* group (Brown and Amadon, 1968). *Buteo brachyurus albigula* differs from the *brachyurus* group in its relatively longer tail and ventral streaking.

Ecology. Frequents forests and forest clearings and edges both in wet regions and in drier areas (but not deserts), preying on diverse animals.

Distribution and variation. Rather discontinu-

ously distributed from Florida and Middle America S to Chile in the W, and to Tucumán and Rio Grande do Sul in the E. Not found in most or possibly all the chaco, but may reach the western fringes, Santa Cruz, Bolivia, and the pantanal from Mato Grosso to central Paraguay. Its range extends approximately from these areas N to the Amazon and Guianas, with a hiatus from there to Venezuela, and E to the Atlantic Coast (S to Rio Grande do Sul). The race occupying South America except for the Andean region (*albigula*) is *B. b. brachyurus*, characterized (Brown and Amadon, 1968) by its very short tail, reduced barring, and (usually) lack of rufous on its neck.

Buteo albicaudatus
White-tailed Hawk

Taxonomy. Polytypic. The most wide-ranging of a group of four, similarly patterned, big-footed New World species comprising a superspecies. Other species include the Andean and southern South American *polyosoma*, northern Andean *poecilochrous* and *galapagoensis* of the Galapagos Islands (see Brown and Amadon, 1968; Mayr and Short, 1970).

Ecology. Generally favors dry woodlands, desert scrub, savannas, and edges of forest, but ranges across grasslands as well. Preys on various animals, chiefly by hovering and then dropping upon them. Partly migratory.

Distribution and variation. New World, southern Nearctic to Buenos Aires. It is replaced by *B. polyosoma-poecilochrous* in western and southern South America. Disjunct populations occur: (1) from Middle America to dry northwestern Venezuela; (2) from the Colombian llanos to the Guianas and the lower Amazon River; and (3) from east-central Bolivia, Mato Grosso and Bahia S to San Juan and southern Buenos Aires. The last-mentioned population is *B. a. albicaudatus*, a large, dark-headed form usually having a black throat. It ranges throughout the chaco and beyond it to some extent (W, only slightly) in all directions.

?*Harpia harpyja*
Harpy Eagle

Taxonomy. Monotypic genus and species.

Known from the Pleistocene of Minas Gerais (Brodkorb, 1964).

Ecology. This large, wide-ranging eagle occupies vast individual territories often including diverse habitats, but chiefly lowland wet forest. Preys upon medium-sized animals, mainly mammals. May wander to S outside breeding range.

Distribution. Middle and South America, S to northern Colombia and E of the Andes, E to Maranhão and Espírito Santo, and S to eastern Bolivia and Mato Grosso. Of doubtful occurrence in the chaco, but may wander into the northern or western portions, and probably has occurred in the fringes of the Bolivian chaco.

Spizastur melanoleucos
Black and White Hawk-eagle

Taxonomy. Monotypic genus and species, related to Old World *Hieraetus* (Brown and Amadon, 1968).

Ecology. An uncommon forest hawk, found about clearings or along edges as well as within forests.

Distribution. Neotropics, from Middle America discontinuously in Colombia, in northern Venezuela, in the Guianas and immediately adjacent Venezuela and Brazil, and S of the Amazon from its mouth throughout eastern and central Brazil to eastern Bolivia, Tucumán, the Paraguayan chaco, eastern Formosa, Misiones, and Rio Grande do Sul. Thus, occurs in the northern chaco, the western edge of the Argentine chaco, and in eastern Formosa.

Spizaetus ornatus
Ornate Hawk-eagle

Taxonomy. Polytypic. Has no close relatives in *Spizaetus*.

Ecology. Found in the moist lowland forests and also somewhat dry forest and edges, feeding on birds and mammals.

Distribution. New World, Middle America S somewhat discontinuously to Tucumán in western Argentina, and to Rio Grande do Sul in the E. *Spizaetus ornatus ornatus* is a weakly defined (pale color) subspecies found from Venezuela and eastern Peru throughout the lowlands S through the Paraguayan chaco and western Argentine sub-Andean forest to Tucumán, and to eastern

Paraguay, Misiones, and Rio Grande do Sul. Thus, it occurs in the northern chaco (Paraguay, Santa Cruz, Mato Grosso), and possibly in the western fringes of Argentina.

FAMILY FALCONIDAE

Polyborus plancus Crested Caracara

Taxonomy. Polytypic. Closely related to other caracaras of this genus, including especially the "*Phalcoboenus*" group. Distinctive within *plancus*, and formerly considered specifically distinct, are: extinct *lutosus* of Guadalupe Island, the Nearctic to northern South American *cheriway* group, and South American *plancus*. The last form differs from the others in its back and breast barring, and in other ways including larger size, and it is also able to occupy cooler regions. Fossil species of *Polyborus* are known from the United States, Mexico, and Puerto Rico.

Ecology. Forages for carrion and opportunistically preys on animals it can secure. Inhabits open country, savannas, and forest edges, nesting in trees or on the ground.

Distribution and variation. New World, from southern fringes of Nearctic to Tierra del Fuego. The distinctive *plancus* ranges S from southwestern Amazonia and the mouth of the Amazon (with a wide gap in between), through Brazil, central Bolivia and Paraguay to Tierra del Fuego, and N on the Pacific Coast to northern Chile. This form occupies the entire chaco, extending beyond it in all directions. There is a gap in Peru and central Amazonia between it and the *cheriway* group of Middle America to Peru, Colombia, the Guianas, and the Amapá region of northeastern Brazil. However, the two forms meet and interbreed about the mouth of the Amazon. Within *P. p. plancus* there is a clinal increase in size southwardly (Brown and Amadon, 1968).

Polyborus chimachima Yellow-headed Caracara and *Polyborus chimango* Chimango Caracara

Taxonomy. Both species polytypic. These two species are very similar structurally and behaviorally, and they replace each other, form-

ing a superspecies (Brown and Amadon, 1968). I consider them insufficiently distinct from *Polyborus* to comprise an essentially monotypic genus *Milvago*. The four "species" of *Phalcoboenus* comprise a superspecies, or in any event they are closely interrelated and extremely similar to *Polyborus* (*sensu stricto*, monotypic). In view of the close relationship among these caracaras (Brown and Amadon, 1968) I see no reason to maintain *Milvago* and *Phalcoboenus* apart from *Polyborus*. *Polyborus chimachima* is whiter than *P. chimango* and lacks barring on the neck and breast and streaks on the head.

Ecology. Both are opportunistic predators and scavengers for all types of carrion; they also take some fruits. *Polyborus chimachima* occupies savannas, woodlands, and forest clearings, and, to a lesser extent, grasslands. More of a woodland species than *P. chimango*, it nests in trees, often at some height, and is not known to nest colonially. *Polyborus chimango* is a grassland, open country, and scrub woodland caracara, nesting in trees or on the ground, and sometimes breeding in loose colonies (Brown and Amadon, 1968). Southern populations of *P. chimango* are to some extent migratory.

Distribution and variation. The superspecies essentially is South American. *Polyborus chimachima* occurs from Panama through northern Colombia and E to the Guianas and northern Amapá, and S along the western edge of Amazonia through Colombia, Peru, and northern Bolivia, and from there NE to the mouth of the Amazon, E to the entire Atlantic Coast of Brazil, and SE to Santa Fe, Corrientes, and northern Uruguay. The weakly differentiated *P. c. chimachima* inhabits the range of the species S of central Brazil. *P. chimango* occurs S from the Paraguayan border of Argentina, Misiones, and Rio Grande do Sul to Tierra del Fuego, and W to the Pacific Coast (where it extends northward to northern Chile). The paler, less heavily marked *P. chimango chimango* occupies the range of the species N of southern Chile, Tierra del Fuego, and Santa Cruz, Argentina. These species overlap narrowly in the southeastern chaco (eastern Formosa to Santa Fe), southeastern Paraguay, Corrientes, and the Rio Grande do Sul-Uruguayan border region. Within the chaco neither of these races seems to occur in the western region

around the Paraguay-Argentine border, but *P. c. chimango* is found S of that in wetter and drier parts of the southern chaco, and it overlaps with *P. c. chimachima* in the southern pantanal region as noted above. The latter form also occurs N from eastern Formosa through the eastern Paraguayan chaco, including the pantanal region, and throughout the Bolivian and Mato Grosso chaco.

Herpethotes cachinnans
Laughing Falcon

Taxonomy. Monotypic genus and species, related to *Micrastur* (Brown and Amadon, 1968).

Ecology. Inhabits forest edges, woodlands, and clearings. Found less commonly in savannas. Feeds mainly on reptiles. Nests arboreally.

Distribution. Neotropics, S from Middle America to Peru in the W and throughout the eastern lowlands to Tucumán, Corrientes, and São Paulo. The southern limit of the species is reached in the southern chaco. It occurs along the western fringes of the Argentine chaco, is lacking in the arid central portion, and recurs in the moist eastern chaco S as far as Chaco and Corrientes. From there it extends N throughout the northern chaco and thence N, NW, and NE.

Micrastur ruficollis
Barred Forest-falcon

Taxonomy. Polytypic, with complex variation and polymorphism. I consider *M. gilvicollis*, often merged in *ruficollis*, as a separate species forming a superspecies with *ruficollis*. *Micrastur gilvicollis* is distinct in plumage pattern and has a shorter tail than *ruficollis*; it is essentially Amazonian, whereas *ruficollis* is a Middle American and subtropical Amazonian fringe form. The two overlap S of Amazonia from Peru to northeastern Brazil. Intergrades are known according to Amadon (Brown and Amadon, 1968), but until more details are available their strong morphological differences, partial sympatry, and general pattern of distribution argue for treating them as separate species (Schwartz, 1972).

Ecology. A large forest falcon, but also at edges and in clearings, and tending to frequent dense vegetation.

Distribution. Neotropics, from Middle America S to Ecuador W of the Andes (where sympatric with *M. plumbeus*, relationships of which

seem to lie with *gilvicollis* or *gilvicollis* and *ruficollis*); a disjunct population occurs in northeastern Colombia and northern Venezuela, and another ranges from eastern Ecuador and Peru through Bolivia to eastern Brazil, and S in the W to Tucumán, and farther E to Chaco and Rio Grande do Sul. *Micrastur ruficollis* is found throughout the northern chaco, and is definitely absent from the south-central and southeastern chaco. It may occur in the western chaco fringes of Argentina (subtropical forest race *olrogii*) and it sporadically inhabits the moist eastern chaco of eastern Formosa and eastern Chaco (in riparian forests and pantanal). Except for the western Argentine chaco, the widespread subspecies *ruficollis*, which is distinguished by color features and size and is smaller than *olrogii*, occupies the chaco range of the species, extending beyond it to the NW (northern Bolivia), N, NE (to Ceará), and E (Atlantic Coast). It is possible that *M. gilvicollis* reaches the northern edge of the Bolivian chaco.

Micrastur semitorquatus
Collared Forest-falcon

Taxonomy. Polytypic, related to *M. buckleyi* with which it is sympatric. Known from Pleistocene deposits in Minas Gerais.

Ecology. A large falcon of forests and forest clearings, frequenting dense thickets in which it darts after prey.

Distribution and variation. Neotropical, from Mexico to Peru and Argentina. In the W, S to Peru and in the E generally inhabits lowlands to Tucumán, Corrientes, and Rio Grande do Sul. The weakly distinguished (pale color) *M. s. semitorquatus* occupies South America from northeastern Colombia E and S. This race inhabits the chaco except for the southern portion, and the central, dry chaco from central western Paraguay southward, and of course it extends beyond the chaco to the N and E.

Spizapteryx circumcinctus
Spot-winged Falconet
Figure 20

Taxonomy. Monotypic genus and species, but closely related to, and possibly congeneric with, African and Asian *Polihierax* (Brown and Amadon, 1968). Probably derived from Africa.

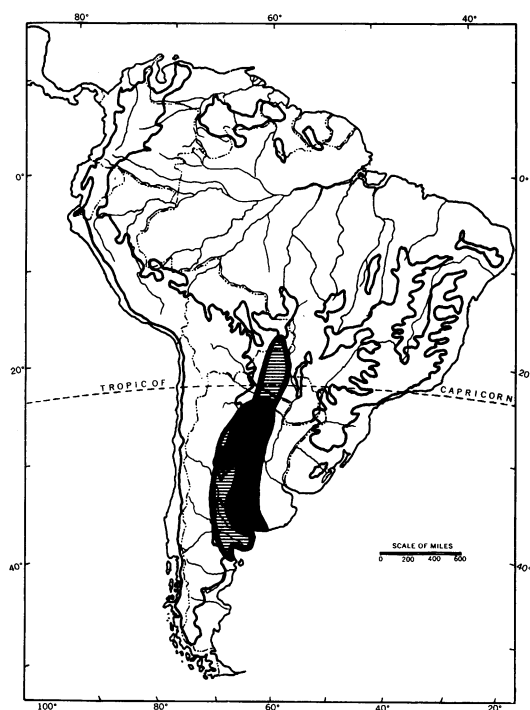


FIG. 20. Range of Spot-winged Falconet (*Spizaipteryx circumcinctus*) in black and of Crested Gallito (*Rhinocrypta lanceolata*) shown by horizontal bars. Both monotypic species frequent dry central chaco and extend south into chaco scrub.

Ecology. Inhabits arid woodlands, mainly dry chaco woods, chaco scrub, and scrub desert, often with open or semi-open areas nearby. To some extent migratory. Feeds on small vertebrates (probably mostly birds) and invertebrates.

Distribution. Endemic in Argentina, from the xeric south-central chaco and arid regions ("montes") just W of the chaco, S through the chaco scrub region W of the pampas to Mendoza and northern Río Negro. Absent from the moist southeastern chaco, occurring in the chaco only in western Chaco, western Formosa, Santiago del Estero, Salta, and Tucumán.

Falco sparverius
American Kestrel

Taxonomy. Polytypic, forms superspecies with *F. tinnunculus* and five other Old World

species (see Mayr and Short, 1970). Fossil from Pleistocene of Minas Gerais, and North America.

Ecology. Inhabits more or less open country, including highland and lowland grasslands, savannas, arid scrub woodlands, chaco, and forest edges and clearings. Feeds mainly on insects and other invertebrates, small mammals, birds, and reptiles usually taken by a plunge from a perch or from a hovering position in the air. Nests in a cavity or crevice (tree, building, holes in banks).

Distribution and variation. Nearctic, Middle America (discontinuously), and South America except for eastern Amazonia and northeastern Brazil. *Falco sparverius cinnamominus* occupies a large area from Peru and northern Bolivia to Tierra del Fuego, W to the Pacific, and E to western Mato Grosso, eastern Paraguay, and Rio Grande do Sul. The southernmost subspecies of this kestrel, it is larger than adjacent races, and it differs somewhat in color. It is found throughout the chaco and beyond it in all directions.

Falco ruficularis
Bat Falcon

Taxonomy. Polytypic. Relationships not fully established in *Falco*.

Ecology. Small, inhabits forest edges, clearings, and woodlands, feeding mainly on bats and small birds, also on insects largely taken while flying. Nests in tree cavities.

Distribution. Middle America and South America: *F. r. ruficularis* occurs from Mexico to Ecuador, northern Argentina, and Rio Grande do Sul. Breeds in the western and northern chaco, and W, N, and E of there. It is absent in the xeric central chaco of Argentina, and from the south-eastern chaco (S of Chaco).

Falco femoralis
Aplomado Falcon

Taxonomy. Polytypic. Known from the Pleistocene of Minas Gerais and of Arizona (Brodkorb, 1964).

Ecology. Diverse habitats, favoring edges and open or semi-open country, but also forest clearings. Probably migratory in the far S. Occurs in temperate South America, but does not penetrate the Nearctic to the same degree. Nests in old nests of other birds (Brown and Amadon, 1968).

Distribution and variation. Nearctic to Tierra del Fuego, almost throughout South America (lacking in parts of Colombia, Venezuela, and the Guianas. An eastern race (*femorialis*) inhabits all of eastern South America, including the chaco, to Tierra del Fuego and southern Chile. This rather weakly marked subspecies (minor color differences, small size) varies clinally, the southern birds being larger and grayer (Brown and Amadon, 1968).

Falco deiroleucus
Orange-breasted Falcon

Taxonomy. Monotypic. I treat this species as an allospecies of cosmopolitan *F. [peregrinus]*, although possibly it is related instead to *F. ruficularis*. *Falco deiroleucus* is the tropical zone representative, "ecologically and perhaps taxonomically" (Brown and Amadon, 1968, p. 847), of *peregrinus*. *Falco peregrinus* occurs throughout the Old World, and in the Nearctic and Mexico, with a widely disjunct race *cassinii* in southern South America (southern Chile to Tierra del Fuego and Falkland Islands). The rare *F. kreyenborgi* of the same area seems allied with the *peregrinus* group rather than the *biarmicus* group, and might even be a color phase of *peregrinus*, as unlikely as that seems (Amadon, personal commun.). It is uncertain whether *cassinii* originated from Nearctic *peregrinus*, or from the Old World (Pacific islands, Africa).

Ecology. A medium-sized falcon of forested mountain slopes, forest edges and clearings, and savannas. Nonmigratory. Preys probably largely on birds taken in flight. Nests in edifices and tree cavities (Brown and Amadon, 1968).

Distribution. New World tropics, discontinuously ranging from Middle America through scattered regions of northern South America (central Colombia; northern Venezuela; southeastern Venezuela and Guianas; and eastern Peru), with a hiatus in Amazonia and most of Bolivia, and then recurring in eastern Brazil S to Rio Grande do Sul, southeastern Bolivia, Paraguay, Tucumán, and Chaco. Within the chaco, occurs sporadically in all but the Argentine xeric central chaco, and the extreme southeastern chaco. From Tucumán, western Paraguay and Chaco Province, extends N through the chaco, NE to the mouth of the Amazon, and E to the Atlantic Coast.

FAMILY CRACIDAE

Ortalis canicollis
Chaco Chachalaca

Taxonomy. Polytypic. Closely related to other species of *Ortalis*, which are largely allopatric with one another.

Ecology. Mainly arboreal, but partly terrestrial. Nonmigratory, almost confined to the chaco.

Distribution and variation. Endemic in central South America occurring in the entire chaco except Corrientes (and Santa Cruz, possibly Bolivia) and extending beyond the chaco slightly to the SW, reaching Córdoba and La Rioja, but otherwise the chaco bounds its range (apparently it crosses the Paraguay River only in northern Paraguay and Mato Grosso). Most of this range is occupied by the smaller, grayer race *canicollis*, with larger *pantanalensis* restricted to the pantanal region of Mato Grosso and presumably adjacent Paraguay and Bolivia. Within *O. c. canicollis* there is a cline of diminishing size and rufous coloration to the S (the species as a whole shows decrease in size to the S), and a cline of increasing grayish color westwardly (Vaurie, 1968).

Penelope obscura
Dusky-legged Guan

Taxonomy. Polytypic, likely forming a superspecies with Guianan to western Amazonian *P. jacquacu*. These have been merged, but were shown to be specifically distinct by Vaurie (1968). *Penelope jacquacu* has red legs and a longer crest, whereas *obscura* is dusky-legged with a shorter crest.

Ecology. An arboreal, nonmigratory species of forests and woodlands.

Distribution and variation. Superspecies endemic to South America. *Penelope jacquacu* occurs in western Amazonia S to northern Bolivia where it may meet *P. o. bridgesi*. *Penelope obscura* occupies a disjunct range just S and SE of *jacquacu*. A lower Andean forest form, *P. o. bridgesi*, probably occurs in the western fringes of the chaco in dense riparian woods (Delacour and Amadon, 1973). The disjunct eastern populations of this species occur in the forests of southeastern Brazil (S from Espírito Santo), northern Uruguay, eastern Paraguay, and north-

eastern Argentina. The southern portion of this range, from Paraguay just west of the Paraguay River, eastern Formosa, eastern Chaco and northern Santa Fe E to Santa Catarina, Rio Grande do Sul, and Uruguay is occupied by *P. o. obscura*. Thus the chaco is inhabited by *bridgesi* in the (wetter) western edges, and by *obscura* in the southeastern region of pantanal and riparian forests. The three races of this species are distinct and not known to intergrade (even the eastern forms which occupy contiguous ranges). Western *bridgesi* is paler brown, less streaked on the back and underparts but more streaked on the wings, and larger. Eastern *obscura* is smaller and much darker with more streaking except for its wings.

Aburria pipile
Common Piping-guan

Taxonomy. Polytypic, including five well-marked races: *pipile*, *cumanensis*, *grayi*, *cujubi*, and *nattereri*, sometimes considered separate species (Delacour and Amadon, 1973). Forms superspecies with parapatric *jacutinga* of southeastern Brazil.

Ecology. Arboreal, forest-dwelling, nonmigratory.

Distribution and variation. Endemic South American, from Trinidad, the Guianas and southern Venezuela W in an arc around Amazonia through eastern Colombia, eastern Ecuador, eastern Peru, and northern Bolivia to central and southern Mato Grosso and northern Paraguay, thence NE to the Lower Amazon. The race *grayi* occupies the northern chaco (northern Paraguay, Bolivian chaco, Mato Grosso), and extends beyond it to the N as far as central Mato Grosso and Peru. It differs from the other races in having a caruncle in place of a wattle on its throat, in its olive-brown gloss dorsally, and in its hirsute crest feathers (Vaurie, 1968).

Crax fasciolata
Bare-faced Curassow

Taxonomy. Polytypic. Seven allopatric species of Middle and South America comprise a superspecies; these include *rubra* (Middle America, northwestern South America), *alberti* (northern Colombia), *daubentoni* (northeastern Colom-

bia, northern Venezuela), *alector* (southern Venezuela, Guianas, northeastern Brazil), *globulosa* (western Amazonia, including eastern Ecuador, eastern Peru, and southeastern Colombia), *blumenbachii* (Espírito Santo, narrow eastern coastal region of Brazil), and *fasciolata* (central Brazil from Amazon mouth S to northern edge of Argentina, W to eastern Bolivia, and E to Minas Gerais). *Crax fasciolata* lacks face wattles, and has white tail tips like *alberti* and *daubentoni* of northern South America. It apparently does not overlap, or meet the other species of this group (Delacour and Amadon, 1973).

Ecology. A ground-foraging but arboreal, large, nonmigratory gallinaceous bird. Much of its range is not heavily forested, so to some extent it inhabits forest edge or woodland.

Distribution and variation. Endemic in South America (see range above). Three rather weakly defined races are based upon largely clinal color variation in females (Vaurie, 1968). The subspecies *fasciolata* occupies all the species' range except east-central Bolivia and possibly northwestern Paraguay, and the region around the Amazon River. It inhabits the northern chaco (except in the far W where *grayi* may occur) and the eastern chaco S to eastern Formosa, eastern Chaco, and northern Corrientes, and from there N to Pará and Maranhão, and NE to Minas Gerais.

FAMILY ARAMIDAE

Aramus guarauna
Limpkin

Taxonomy. Monotypic genus, polytypic species.

Ecology. Forages on snails and invertebrates. Inhabits large marshes and swamps. Nonmigratory.

Distribution. New World, from southern United States to Ecuador and central Argentina. *Aramus guarauna guarauna* inhabits all the South American range, occurring from Panamá to Ecuador in the W, and in the E throughout the lowlands S to La Rioja, Córdoba and Buenos Aires, Argentina, and Uruguay. This form is found in wet areas throughout the chaco, although it may be absent in the dry portions; it is particularly common in the pantanal.

FAMILY RALLIDAE

Rallus sanguinolentus
Plumbeous Rail

Taxonomy. Polytypic species. Very closely related to *R. nigricans*, and forming a superspecies with it. *Rallus nigricans* occupies widely disjunct areas: southwestern Colombia; eastern Ecuador and eastern Peru; and eastern South America from Pernambuco S to eastern Paraguay, Misiones, and Rio Grande do Sul. It overlaps with *sanguinolentus* over a small area of central-eastern Paraguay. These rails are very similar, but *sanguinolentus* has a dark bill with a red basal spot and little or no white in the throat, whereas *nigricans* has a yellowish bill lacking the red spot, and a discrete white throat.

Ecology. Wet areas of all kinds, from tiny streams to marshes and swamps, and in diverse habitats from woodlands to puna and pampas. Forages in and near water for small invertebrates. Nests on the ground or in marsh vegetation.

Distribution and variation. Superspecies endemic in South America. *Rallus sanguinolentus* occurs from western and central Peru S along the Andes to Tierra del Fuego, and from there N in the E to the northern chaco, eastern Paraguay, Corrientes, and Rio Grande do Sul; a disjunct local population occurs in Rio de Janeiro, within the range of *R. nigricans* (the status and relations with *nigricans* are in need of studies based on field work, which might help to establish whether it represents a rather recent or an ancient range extension). *Rallus sanguinolentus* occurs sympatrically with the forest-inhabiting *nigricans* in eastern Paraguay (specimens from same locality) without interbreeding. *Rallus sanguinolentus sanguinolentus* occurs in all but the northern chaco (no records from eastern Bolivia or the pantanal of Mato Grosso), and from there through the northeastern range of the species S to Río Negro. The several races of this species are disparate in size, and show minor color variation; *R. s. sanguinolentus* is small, rather pale, and with dark dorsal spots.

Rallus maculatus
Spotted Rail

Taxonomy. Relationships of this polytypic species are uncertain, although it clearly belongs in *Rallus*.

Ecology. Frequents marshes of all sizes in forested and unforested regions, but not in Amazonian forests. Nonmigratory.

Distribution. New World, West Indies and Mexico discontinuously to northern Buenos Aires. The race *maculatus* occupies the South American portion of this range, to wit: northwestern Peru; Colombia along the coast to the Guianas; and, Pará and Ceará S through campos, caatinga, and coastal areas to Salta, Tucumán, Córdoba, northern Buenos Aires, and Uruguay. It occurs in suitable areas of the chaco except for northwestern Paraguay and Bolivia (where it ultimately may prove to occur), and probably most of the arid central chaco of Argentina.

Armidés cajanea
Gray-necked Wood-rail

Taxonomy. Polytypic, relationships not established fully within *Aramides*. It is known from the Pleistocene of Florida, where it does not now occur (Brodkorb, 1967).

Ecology. Inhabits marshes, swamps, borders of large and small streams; wanders out from thickets in such places into surrounding forests or open country (savannas, northern pampas). Nonmigratory.

Distribution. New World, presently Middle America and South America as far S as northern Buenos Aires. From Panama to northern Colombia and E of the Andes throughout Amazonia and S to Tucumán, northern Buenos Aires, and Uruguay *A. c. cajanea* occurs. It is generally distributed throughout the chaco, but doubtless is lacking in much of the south-central portion.

Aramides ypecaha
Great Wood-rail
Figure 21

Taxonomy. Monotypic species, relationships within *Aramides* not worked out.

Ecology. Generally occurs in marshes and esteros, but may forage far from water. Nonmigratory.

Distribution. Endemic in South America, peculiarly (for a rail) disjunct in eastern Brazil (Bahia, Piauí, Minas Gerais), in eastern Mato Grosso, and from central Paraguay and Misiones S through the eastern chaco and wet pampas to Buenos Aires, and E to Rio Grande do Sul and

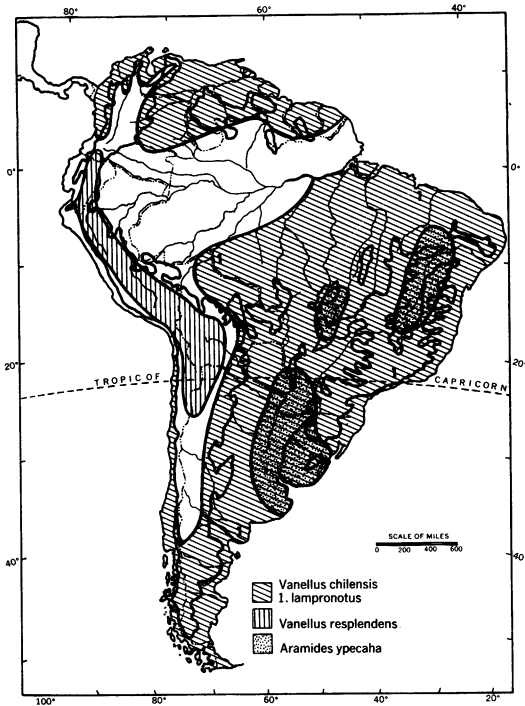


FIG. 21. Range of Great Wood-Rail (*Aramidides ypecaha*) and Southern Lapwing (*Vanellus chilensis*). Monotypic rail shows a caatinga-campo-pampas distribution, but with disjunction presumably due to increasing aridity fragmentation. *Vanellus chilensis* forms a superspecies with Andean *V. resplendens*, range of which is shown. Distribution of *chilensis* is that of a widespread lowland species of open and partly forested country; it is absent only from Amazonian forests, Andean uplands, and arid west coast, with a racially disjunct northern population.

Uruguay. Within the chaco it seems restricted to the southern pantanal region, from north-central Paraguay S, and beyond the chaco to the E and S.

Porzana albicollis
Ash-throated Crake

Taxonomy. Polytypic species. Known as a fossil from Minas Gerais (Pleistocene; Brodkorb, 1967).

Ecology. Inhabits small marshland and wet grassland, occurring in forest and savanna regions. Nonmigratory.

Distribution and variation. Endemic in South

America, discontinuously found in Colombia, eastern Colombia to the Guianas, the lower Amazon, northwestern Argentina, northern Bolivia through the eastern chaco to the delta of the Rio de la Plata, and from Paraíba to southern Goiás and Rio de Janeiro. The larger, darker (brownier) of the two races, *albicollis*, occurs S of the Amazon (three disjunct populations). Within the chaco it occurs throughout the moist eastern portion, and perhaps in the western fringes (Tucumán).

Poliolimnas flaviventer
Yellow-breasted Rail

Taxonomy. Polytypic species. Recently removed from *Porzana* and placed in *Poliolimnas* (Olson, 1970), with one other species, *P. cinereus*, of Pacific islands.

Ecology. Little-known, inhabits marshland.

Distribution. New World, spottily distributed from Mexico and the West Indies to northern Buenos Aires. In South America found in northern Colombia, and (*P. f. flaviventer*): southern Colombia; Venezuela and the Guianas; northwestern Brazil; eastern Brazil from the mouth of the Amazon to Bahia and Minas Gerais; central Paraguay; Tucumán; and Santa Fe and Buenos Aires. Thus, it is known from the eastern Paraguayan chaco (in the pantanal), and possibly the southwestern edge (Tucumán) and southeastern edge (Santa Fe) of the chaco. The subspecies *flaviventer* is distinct, having blacker upperparts with more white spotting than other races.

Neocrex erythrops
Paint-billed Crake

Taxonomy. Monotypic genus, polytypic species, possibly congeneric with *Porzana*.

Ecology. Found in small to large marshes in diverse (forested, unforested, lowlands, highlands) habitats, including the chaco.

Distribution and variation. Mainly South American (Panama also). Three well-differentiated races (a new form related to *columbianus* recently was described from Panama by Wetmore, 1967). Of the races, *columbianus* of western and central Colombia and western Ecuador has been considered specifically distinct. *Neocrex erythrops erythrops* occupies central-western Peru. *Neocrex erythrops olivascens*, smaller in

size, darker generally and browner above with less white in the throat and barring under the wings compared with *erythroptis*, is found from the lower Amazon SW to Tucumán, S to Mato Grosso and Paraguay, and SE to Espírito Santo, and a northern disjunct of this race occurs in the llanos of Colombia and Venezuela to the mouth of the Orinoco River. Found in the Paraguayan chaco, the pantanal of Mato Grosso, and probably the western fringe of the Argentine chaco (Salta, Tucumán), and from there to the W (in Argentina), and to the E and N.

Porphyriops melanops
Spot-flanked Gallinule

Taxonomy. Monotypic genus, polytypic species.

Ecology. Streams, lagoons, small ponds, wet grasslands. Not well known. Possibly migratory to some extent.

Distribution and variation. Endemic in South America, discontinuously distributed in the Andes of Colombia; possibly Peru; central Chile; eastern Bolivia to Mendoza, Buenos Aires, Uruguay, and Rio Grande do Sul; and in eastern Brazil from Ceará to São Paulo. The last two disjuncts comprise a single race, *melanops*. This form is found in the entire chaco except possibly Mato Grosso, and from there E, S, and SW. The three subspecies are weakly defined, *melanops* being small with a proportionally longer bill than *crassirostris* (Chile to Santa Cruz, Argentina) and *bogotensis* (Colombia).

Laterallus melanophaius
Rufous-sided Crake

Taxonomy. Polytypic species, related to several species including *leucopyrrhus*.

Ecology. Wet grassy or marshy areas, including grass along small streams. May occur in dry grasslands near such streams. Feeds on insects, other invertebrates. Nonmigratory.

Distribution and variation. New World, Middle America, spottily through South America to Buenos Aires. The *albigularis* group, which has been considered specifically distinct, occurs from Middle America to northern and western Colombia and western Ecuador. Two races comprise the *melanophaius* group. *Laterallus melanophaius*

oenops occupies western Amazonia. *Laterallus melanophaius melanophaius* includes disjunct populations in northern Venezuela, the Guianas, and eastern Venezuela, and from the mouth of the Amazon through eastern Brazil to eastern Bolivia, La Rioja, Buenos Aires, and Uruguay. This form occurs throughout the chaco in marshes, esteros, riverbanks, and islands, and in grassy areas along major and minor streams. From the chaco it extends NE, E, and S. *Laterallus melanophaius melanophaius* is characterized by rufous ear coverts but little rufous on the face, gray lores, darker overall coloration and dusky dorsal color.

Gallinula chloropus
Common Gallinule

Figure 22

Taxonomy. Polytypic. Related to *G. angulata* (Africa) and *G. tenebrosa* (Australia) (Mayr and Short, 1970). Known as a fossil from Minas Gerais (Pleistocene; Brodkorb, 1967).

Ecology. Occurs about ponds, lakes, swamps, marshes, feeding both in or near the water and on land back from the water. Nests in reeds or marsh grass. Partly migratory.

Distribution and variation. Nearly cosmopolitan, including much of the New World. In South America *pauquilla* occurs (from Middle America) in northern and western Colombia to western Peru, *garmani* is found in the central Andes (Peru to Jujuy, Argentina), and *galeata* is found disjunctly in northern Venezuela and the Guianas, and from near the mouth of the Amazon SE, and then S and W to Mato Grosso, eastern Bolivia, La Rioja and northern Buenos Aires, Argentina, and Uruguay. The last subspecies is found in suitable sites throughout the chaco, and from there W (slightly), N (slightly), E and S. *Gallinula chloropus galeata* has paler legs, shorter wings, and a smaller bill shield than adjacent races.

Porphyryula martinica
Purple Gallinule

Taxonomy. Monotypic species. No very close relatives in its genus.

Ecology. Found in lagoons, esteros, swamps, and marshes. Nonmigratory.

Distribution. New World, from southern

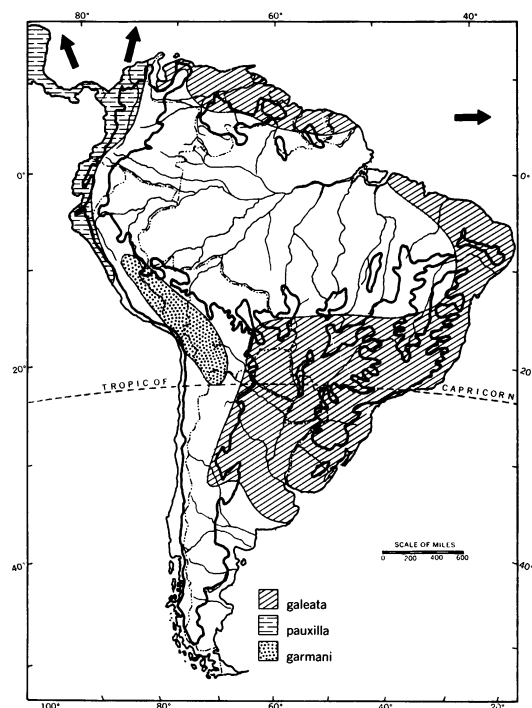


FIG. 22. Range of Common Gallinule (*Gallinula chloropus*). There are two racially disjunct South American populations, in Andes and in lowland southeast plus northern coast. Favors large wet areas in open country or forests other than those of Amazonia. Arrows indicate direction in which ranges extend.

North America through Middle America and the West Indies S to Tucumán, Santa Fe, and Buenos Aires, Argentina, and western Uruguay. It occurs in western South America S to Peru, and throughout the eastern lowlands to the southern chaco, Buenos Aires, western Uruguay, and Rio Grande do Sul. The chaco forms the southwestern corner of the species' range which extends slightly W (subtropical forest along Andes) and SE (Buenos Aires), and to the N and E.

Porphyryla flavirostris
Little Gallinule

Taxonomy. Monotypic species, no very close relatives in its genus.

Ecology. Small, frequents extensive marshlands, not well known.

Distribution. Endemic in South America, essentially Amazonian (although apparently missing from the central Amazon area). Occurs from the Orinoco River to the mouth of the Amazon, W to eastern Colombia and eastern Ecuador, and S in central South America to northern Bolivia, the Paraguay River area of Paraguay and immediately adjacent Argentina (Formosa), eastern Mato Grosso, and Minas Gerais. Within the chaco, which forms its southern range limit, it occurs only in the pantanal region of Mato Grosso, Paraguay, and eastern Formosa.

Fulica armillata
Red-gartered Coot

Taxonomy. Monotypic species, nearest relative among coots uncertain.

Ecology. Inhabits marshes, esteros, lakes, and lagoons, where it forages along the shores and in the water while swimming. Constructs nest in floating or semi-floating vegetation.

Distribution. Endemic in southern South America. Ranges from central Chile S to Tierra del Fuego and N east of the Andes to Paraguay and coastally to Rio de Janeiro. It is found in the southern chaco (N to the central Paraguayan chaco) and from there E, S, and slightly to the W.

Fulica leucoptera
White-winged Coot
Figure 23

Taxonomy. Monotypic, the southern New World representative of the superspecies *Fulica atra*, which includes Old World *atra* and New World *caribaea* and *americana*. *Fulica leucoptera* shows more white in the wings than do the other species, it is smaller in size, and its bill and round frontal shield are lemon yellow (*americana*, which barely overlaps with *leucoptera* in northern Chile is larger, with little or no white in the wing, a white bill with yellowish edges, and a round reddish frontal shield).

Ecology. Like other coots.

Distribution. Endemic in southern South America from northern Chile, the Argentine Andes, lowland eastern Bolivia, eastern Paraguay, and Rio Grande do Sul S to Tierra del Fuego. It occurs throughout the chaco in large wet areas

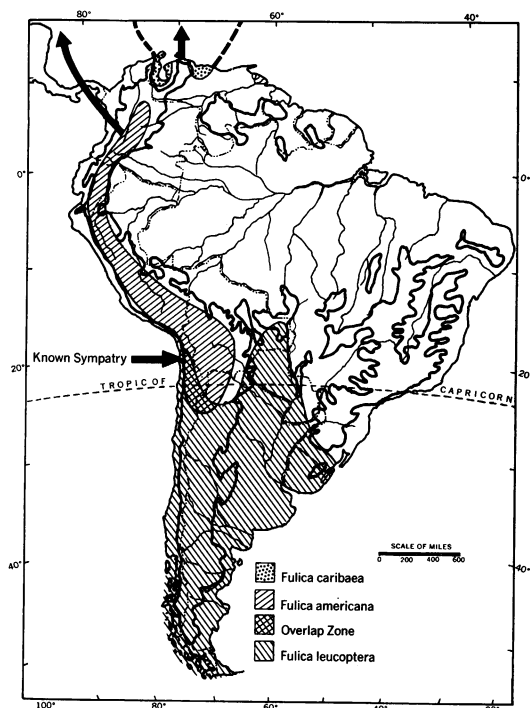


FIG. 23. Range of White-winged Coot (*Fulica leucoptera*), also showing part of ranges of two of its allospecies, *F. americana* and *F. caribaea*. *Fulica leucoptera* is a temperate bird of wet places, reaching its northern limit at the northern chaco border. It slightly overlaps with *F. americana*, as indicated. Arrows at top of map indicate ranges extending north.

(esteros and marshes), the chaco forming the northern extreme of the species' range. The Andean population of *F. americana* occurs S to northern Catamarca, Argentina, and northern Chile. It is known to breed sympatrically with *leucoptera* on certain lakes in Tarapacá, Chile.

Fulica rufifrons
Red-fronted Coot

Taxonomy. Monotypic. Relationships not clearly established with other coots.

Ecology. Ponds, lakes, lagoons, marshes, as other coots; nests in floating vegetation.

Distribution. Endemic in South America, from northern Chile to central Chile, E into Argentina, from there S to northern Tierra del Fuego, and N to the southern fringe of the chaco

and to Uruguay. Breeds sporadically in the eastern Paraguayan chaco (Campo Esperanza), and possibly in the southeastern moist chaco. Thus, known in the chaco only in Paraguay and northern Santa Fe.

FAMILY CARIAMIDAE

Cariama cristata
Red-legged Seriema
Figure 24

Taxonomy. Monotypic genus and species, perhaps congeneric with the smaller *Chunga burmeisteri*, its only extant relative. Reported

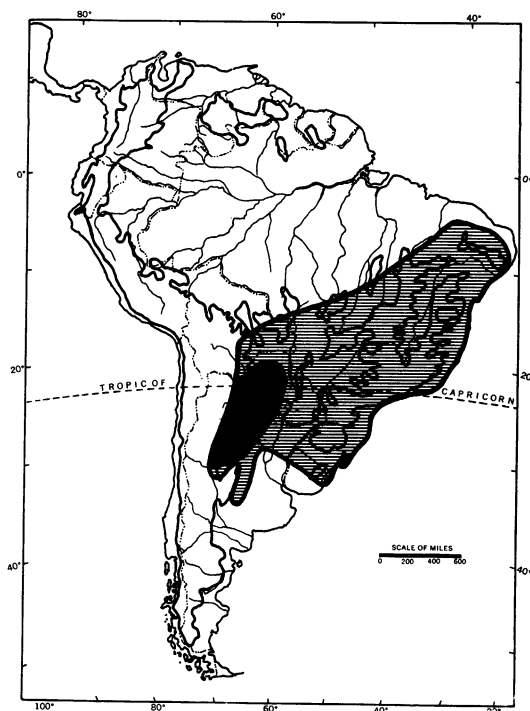


FIG. 24. Range of Red-legged Seriema (*Cariama cristata*) shown by horizontal lines, and Black-legged Seriema (*Chunga burmeisteri*) shown in black. Latter occurs mainly in central and western chaco but ranges westward into xeric parts of dry subtropical forest. *Cariama cristata* is chaco-campo-caatinga species that occurs also in dry subtropical forest and open parts of southeastern Brazilian forest. Both are monotypic.

from the Pleistocene of Minas Gerais (Brodkorb, 1967).

Ecology. Nonmigratory. Strides through open woodlands of all types and savannas, feeding on small animals. Nests in trees.

Distribution. Endemic in south-central South America. Found from Ceará S through the caatinga and forested southeastern Brazil to Uruguay, SW to eastern Bolivia, and San Luis and La Pampa, Argentina. It is common throughout the chaco, and beyond it in all directions except SE (does not occur in the pampas).

Chunga burmeisteri
Black-legged Seriema
Figure 24

Taxonomy. Monotypic genus and species. A close relative of, perhaps congeneric with, the larger *Cariama cristata*.

Ecology. Inhabits dry woodland, savanna, and brushy scrub, is terrestrial and nonmigratory, and nests in trees.

Distribution. Endemic in south-central South America. Found in the chaco, except the southeast, the eastern pantanal, and the northern region (northern Paraguay, Bolivia). Extends beyond the chaco to the W (arid scrub or "monte," parts of subtropical forest) and SW to San Luis.

FAMILY JACANIDAE

Jacana jacana
Wattled Jacana

Taxonomy. Polytypic. Forms a superspecies with Middle American *J. spinosa*. These species probably were derived from Africa ("Actophilornis" of Africa and Madagascar is very closely allied, and downy young of that genus are about identical with those of the jacanas); the group is well developed in the Old World, but represented only by this superspecies in the New World. *Jacana jacana* differs from *J. spinosa* in having only a two-lobed (vs. three-lobed) frontal shield, in the presence of a lappet at the corner of the bill, and in bill and frontal shield color. The two overlap by some 50 km. in Panama, and at least a few hybrids occur (Wetmore, 1965). *Jacana jacana* is known from Pleistocene deposits in Minas Gerais (Brodkorb, 1967).

Ecology. Inhabits vegetation floating on and growing from water; edges of lagoons, swamps, esteros, and lily-pad overgrown ponds. Nests in swamp vegetation. Nonmigratory.

Distribution and variation. Essentially South American, extending into southern Panama where it overlaps with *J. spinosa*. Occurs S to Peru in the W, and in the E through lowlands S to La Rioja, northern Buenos Aires, and Uruguay. *Jacana jacana jacana* inhabits eastern South America from eastern Venezuela, central Amazonia, and eastern Bolivia E to the Atlantic Coast, and S to the limits of the species' range. Thus, this race occurs throughout the chaco in wet areas (it is lacking in much of the chaco), extending beyond it to the N, E, S, and slightly to the W (subtropical dry forest at base of Andes). The subspecies *jacana* is rufous rather than chestnut or black on the back as in other races, and it lacks black in the scapular region and the mantle.

FAMILY ROSTRATULIDAE

Nycticryphes semicollaris
South American Painted Snipe

Taxonomy. Monotypic genus and species, one of two species in its family (other species in Africa-Asia).

Ecology. Inhabits wet grassy areas around esteros, marshes.

Distribution. Endemic in south-central South America. Occurs from the central chaco (Paraguay) SE to Uruguay and Rio Grande do Sul, S to Río Negro and in the W to central Chile, and W to the subtropical dry forest region. The chaco forms its northern extreme range, and it is found S from there. It is most common in the wet eastern chaco, but is found in suitable areas in the central and western chaco as well.

FAMILY CHARADRIIDAE

Vanellus chilensis
Southern Lapwing
Figure 21

Taxonomy. Polytypic species. With *resplendens*, represents an invasion of the New World of *Vanellus*, probably from Africa (possibly the ancestor of *V. vanellus*), separate from that of

ancestral *V. cayanus* (Bock, 1958). The genus is well developed in the Old World, especially in the tropics. *Vanellus resplendens* and *V. chilensis* comprise a superspecies; although they have been separated generically they are very similar in vocalizations, behavior, and color pattern (personal observ.; see also Bock, 1958), and they have complementary ranges. *Vanellus resplendens* occurs in the central Andean highlands (southern Colombia S to northwestern Argentina and northern Chile). The latter species shows a reduction of sharply contrasting patterns, the loss of face patch and crest feathers, replacement of purple for green on the wing coverts, replacement of black by gray on the breast, and its bill is thinner compared with *chilensis*, which is known from Pleistocene deposits in Minas Gerais and Buenos Aires (Brodkorb, 1967).

Ecology. Rather typically lapwing-like, aggressive, loudly challenging trespassers in its domain. Nests on ground in grasslands, savannas, cultivated fields, edges of marshes.

Distribution and variation. Endemic over much of lowland South America, discontinuously. Occurs from northern Colombia through the llanos of Colombia and Venezuela, and the Guianas, S of which there is a hiatus; it then recurs from southern Amazonia and the lower Amazon River through southern Brazil, northern and eastern Bolivia, Paraguay, Uruguay, all of lowland Argentina and most of Chile (except northern edge and northern mountains). Its range includes the Andes W of Patagonia. The large race *lampronotus*, distinguished by minor features of size and color, occurs throughout the chaco in wet areas, grassy areas, pastures, and cultivated regions, and beyond the chaco N to the Amazon, E to the Atlantic Coast, W to the lower foothills of the Andes, and S to Río Negro.

Vanellus cayanus
Pied Lapwing

Taxonomy. Monotypic species, related to Old World *Vanellus* separately from the *chilensis* superspecies, and derived from Africa (Bock, 1958).

Ecology. A riparian and woodland swamp lapwing. Nonmigratory. Feeds on insects and small invertebrates.

Distribution. Endemic in South America,

chiefly in Amazonia and the Orinoco basin. From Venezuela and eastern Colombia through the Guianas and northern Brazil to the Amazon and beyond through eastern Peru, northern Bolivia, and Amazonian central Brazil (E to campos of Goiás), S to eastern Bolivia, northern Paraguay, Misiones, and Paraná. Within the chaco it is restricted to the pantanal of Mato Grosso and northern Paraguay, to the northern fringe of the Paraguayan chaco, and to Santa Cruz, Bolivia. This region forms the southwestern edge of the species' range.

Charadrius collaris
Collared Plover

Taxonomy. Monotypic species, relationships in *Charadrius* uncertain, but perhaps with Andean *C. alticola* and cosmopolitan *C. alexandrinus* (Bock, 1958).

Ecology. One of few small tropical plovers, inhabiting sandy and muddy beaches coastally and along river edges and on islands and sand bars in rivers. Nests on ground along sandy, gravelly, or muddy stretches of beach. Nonmigratory.

Distribution. New World, Mexico to central Argentina. Occurs S to Ecuador in the W, and E of the Andes S through the lowlands to La Rioja, Buenos Aires, and Uruguay. It is locally distributed along major rivers in the central chaco, and especially in the eastern and western chaco. Extends beyond the chaco slightly to the S and W, and throughout areas to the N and E.

FAMILY SCOLOPACIDAE

Gallinago gallinago
Common Snipe

Taxonomy. Polytypic. Includes Old World *gallinago* group, North American *delicata*, South American *paraguaiae*, and southern South American *magellanica*. These form a superspecies with central Andean (Peru to northwestern Argentina) *andina*, which was formerly merged in *paraguaiae* as a species apart from *gallinago*. Relationships among snipes are difficult to establish because of great plumage similarities.

Ecology. Marshes, wet grasslands, nesting on ground. Partly migratory.

Distribution and variation. Nearly cosmopoli-

tan, in South America breeding from coastal Venezuela (*delicata*) and inland Venezuela (*paraguaiiae*) S in lowlands to San Juan, Buenos Aires, and Uruguay and (*magellanica*) from northern Chile and Neuquén, Argentina, S to Tierra del Fuego. *Gallinago gallinago paraguaiiae* breeds throughout (locally) the chaco in wet, grassy areas, and beyond the chaco it extends slightly to the W, far to the N and E, and S into the northern pampas. This race is distinguished by underwing barring, color tone (paler), and barring of its sides from other races; its wings also are more rounded.

?*Gallinago undulata*
Giant Snipe

Taxonomy. Monotypic species, relationships unclear within *Gallinago*.

Ecology. Favors savanna and woodland edges. Little known, local, and perhaps rare (as well as secretive).

Distribution. Endemic in South America; discontinuously distributed in central Colombia, in northern and eastern Venezuela, the Guianas, adjacent northern Brazil, and easternmost Colombia, and from Mato Grosso and Rio de Janeiro to eastern Paraguay and northern Uruguay. It probably occurs in the fringes of the chaco of eastern Santa Cruz, Bolivia, and in the northeastern corner of the Paraguayan chaco, but not certainly reported within the chaco.

FAMILY RECURVIROSTRIDAE

Himantopus melanurus
White-backed Stilt

Taxonomy. Monotypic (see below). One species of a complex of up to eight species (Mayr and Short, 1970) forming a worldwide superspecies. Some of these, but not all, probably will prove conspecific, but comparative studies are needed to evaluate them. The North American and Middle American *H. mexicanus* reaches South America (northern Peru and the region north of the Amazon River). *Himantopus melanurus* differs from *mexicanus* in its white crown and forehead (*mexicanus* is black-capped) and the white across its back.

Ecology. Wet areas: marshes, lake-shores, lagoons, with relatively clear borders. Wades in

shallow water to forage for small invertebrates. Migrates northward for the winter.

Distribution. Endemic in southern South America. Occurs from central Chile E to northern Río Negro, Buenos Aires, Uruguay, and Rio Grande do Sul, and N to Santiago del Estero and Corrientes. The chaco is occupied only along the southern fringes, mainly in the pampas-chaco ecotone, and in lagoons and esteros elsewhere. This region forms the northern border of the species' breeding range, as far as is known (Olrog, 1968). However, the status of peculiarly colored birds (in the American Museum of Natural History collection) from northeastern Brazil is unclear. Some specimens appear intermediate between *melanurus* and *mexicanus*, and there may be a somewhat intermediate (hybrid?) population inhabiting that region.

FAMILY LARIDAE

Larus cirrocephalus
Gray-hooded Gull

Taxonomy. Polytypic. Forms superspecies with *L. bulleri* and *L. novaehollandiae* of the Asian region (see Moynihan, 1959).

Ecology. Nests along coast and on islands in major rivers, wandering overland and up minor tributaries in search of food; omnivorous.

Distribution. African and South American, likely derived from Africa, as its relatives are Old World species. The South American race *cirrocephalus* breeds from Rio de Janeiro to southern Buenos Aires coastally, and inland along the Paraguay-Parana river and the Uruguay River, and possibly their major tributaries. It also breeds in coastal Peru. From centers along the Río Paraguay (possibly also the lower Pilcomayo and Bermejo rivers), and possibly lagoons elsewhere in the chaco, these gulls wander across and throughout the chaco, and as far as the base of the Andes.

Phaetusa simplex
Large-billed Tern

Taxonomy. Polytypic species; monotypic genus of uncertain affinities.

Ecology. Restricted to the coast and major rivers, foraging for fishes in open water. Nests on islands in rivers.

Distribution and variation. Endemic in South America. An isolate occurs in western Ecuador; otherwise ranges from northern Colombia through the lowlands of central and eastern South America to Uruguay and northern Buenos Aires. The weakly defined (grayer above and on tail), clinally intergradient southern race *chloropoda* occurs approximately from central Amazonia and eastern Brazil S along the eastern fringe of Bolivia and through eastern Paraguay and the eastern chaco to Buenos Aires, and E to the Atlantic Coast. It breeds along the Paraguay-Parana river and forages westward into the central chaco along major rivers (Bermejo, Pilcomayo, probably eastern portions of others in the breeding period, which is in the rainy season).

Sterna superciliaris
Yellow-billed Tern

Taxonomy. Monotypic species. An element of the nearly cosmopolitan *albifrons* superspecies, including *S. lorata* (western South America from Ecuador to northern Chile, coastally), *S. nereis* (Australian area), *S. albifrons* (North and Middle America, West Indies, Trinidad, Old World), and *S. superciliaris* (Mayr and Short, 1970). *Sterna superciliaris* is similar to *albifrons* in size and color generally, but it has a heavier bill which is yellow, lacking the dark tip of *albifrons*; its loral mark is narrow but complete, and its legs and feet are olive, not yellow as in *albifrons*. *Sterna albifrons* has a broad, complete loral mark. Western South American *lorata* is smaller than *albifrons* and *superciliaris*, it is grayer below, its bill is darker with a large black tip, and the bill is thinner than in the other two species just mentioned. *Sterna nereis* is larger than the other three species, and unlike them, it has an incomplete loral mark; its wings are gray (replaces black of others), it is very white above, and its bill is like that of *albifrons*, but somewhat larger and with the black tip reduced or wanting.

Ecology. Frequenting rivers, the coast, diving for small fishes, and nesting on beaches, usually on islets inland.

Distribution. Endemic in lowland eastern South America, from coastal Venezuela through the Guianas, Amazonia, the northern edge of Bolivia, and all of eastern and southern Brazil to

Uruguay and northeastern Argentina. Found in the immediate vicinity of the Paraguay River and the lower Pilcomayo River (also lower extremes of other chaco rivers) in the eastern chaco, but otherwise lacking from that region.

FAMILY RYNCHOPIDAE

Rynchops nigra
Black Skimmer

Taxonomy. Polytypic, comprises a superspecies with African *flavirostris* and Indian *albicollis* (Mayr and Short, 1970). Probably derived from Africa.

Ecology. Forages on the coast and in rivers for fish using its laterally compressed bill by "skimming," that is, dragging its lower bill through the water.

Distribution and variation. New World, somewhat discontinuously. In South America an isolate occurs in western Ecuador; otherwise, found from northern Venezuela E and S coastally, and along rivers of the Orinoco and Amazon system (W to eastern Colombia, eastern Peru), through central Brazil to the Paraguay-Parana river, the Rio de la Plata, Buenos Aires (northern coast), and Uruguay. Within the chaco it is confined to the Paraguay River, and the broader, lower (eastern) portions of major trans-chaco rivers.

FAMILY COLUMBIDAE

Columba speciosa
Scaled Pigeon

Taxonomy. Monotypic. Forms a superspecies with West Indian (to islands off Venezuela) *C. squamosa* (both in turn are related to *C. leucocephala*; Goodwin, 1967). Both have similar bills, color of the orbital bare skin, and head coloration. *Columba speciosa* differs from *squamosa* in having ventral barring (squamous), rufous replacing gray on the back, and in other ways.

Ecology. Nests in trees; inhabits forest edges, and clearings, open woodland, and savannas. Territorial when nesting, otherwise social.

Distribution. Middle America and South America, S to Ecuador in the W, and to north-central Argentina in the E. Occurs throughout lowland eastern South America S to eastern Boliv-

ia, Paraguay mainly in the E and along the Paraguay River, Argentina along the Paraguay-Parana rivers to Santa Fe, in Misiones, and Santa Catarina. Found in the eastern edge of the chaco, mainly in riverine timber but foraging throughout the pantanal, S to Santa Fe.

Columba picazuro
Picazuro Pigeon
Figure 25

Taxonomy. Polytypic. Comprises a superspecies with northern Colombian-coastal Venezuelan *C. corensis* (Goodwin, 1967). These species are closely related, possibly even conspecific. *Columba picazuro* is darker than *corensis*, with a dark bill (rather than a pale bill), white under the tail and gray under the wings. Both have the same

general coloration, neck markings, wing pattern, and tail pattern.

Ecology. Inhabits semiwooded country-savannas, chaco, caatinga, and the northern pampas. Flies long distances into open country and cultivated area from woodlands required for nesting purposes. Lays one egg in a loose tree nest. Migrates from southern portion of its range for the winter, occurring in large bands (Olrog, 1968).

Distribution and variation. Endemic in south-central South America. Disjunct populations occur in the caatinga region (*marginalis*) and from eastern Bolivia and western Mato Grosso S through the chaco, the Andean foothills and eastern Paraguay to Mendoza, La Pampa, Buenos Aires, Uruguay, and Rio Grande do Sul (*C. p. picazuro*). The chaco forms the northern portion of this latter range, although *picazuro* does extend slightly beyond the chaco in northern Santa Cruz and southwestern Mato Grosso. This race occupies the entire chaco, and beyond it to the W slightly (subtropical forest edges, "monte"), to the S, and eastward to the dense, continuous southeastern Brazilian forest.

Columba maculosa
Spot-winged Pigeon

Taxonomy. Polytypic. Closely related to the sympatric *C. picazuro* and *C. speciosa* (Goodwin, 1967).

Ecology. Nests in trees, inhabiting open country both in the highland puna, and in chaco, pampas, desert scrub, and woodland edges in the lowlands. Like most pigeons mainly a seed-eating species, foraging on the ground.

Distribution and variation. Endemic in South America, from highland southern Peru and Bolivia through the eastern Andean slopes of eastern Bolivia to Neuquén, Argentina, and adjacent lowlands from the northern chaco to Rio Grande do Sul, Uruguay, Buenos Aires, and Río Negro. The highland Bolivian race *albipennis* is longer-billed with more spots and a white wing stripe lacking in the lowland subspecies *maculosa*. The latter inhabits all parts of the chaco except the pantanal of Mato Grosso and adjacent Santa Cruz and Paraguay. It extends southward from the chaco through the area described above.

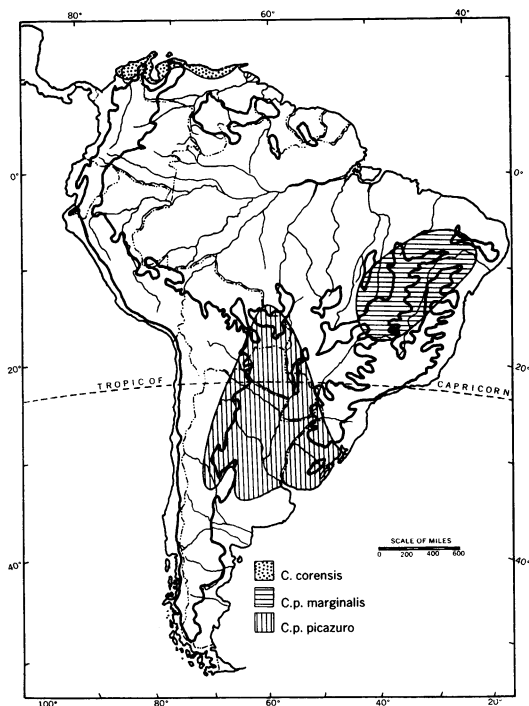


FIG. 25. Range of Picazuro Pigeon (*Columba picazuro*) and its allospecies *C. corensis*. *Columba picazuro* has disjunct races in caatinga region and chaco-pampas-dry subtropical forest area, and *corensis* is isolated in arid coastal Venezuela and Colombia.

Columba cayennensis
Pale-vented Pigeon

Taxonomy. Polytypic. Rather closely related to the *C. flavirostris* group (Goodwin, 1967).

Ecology. Usually lays one egg in a tree nest. Frequents all types of forest and woodland, including savannas, chaco, and Amazonian wet forest. Forages in trees and on the ground. Non-migratory.

Distribution and variation. New World, Middle America to western Ecuador, and E of the Andes to the southern chaco and Uruguay. Several ill-defined races are recognized, including *C. c. sylvestris*, which has more distinct tail barring than other forms. This race occupies the entire chaco, favoring dense vegetation where it is available; it extends slightly W into the forested foothills of the Andes, E to Uruguay and the Atlantic Coast of Brazil, and N to the Amazon River.

Zenaida auriculata
Eared Dove

Taxonomy. Polytypic. The South American representative of the North and Middle American *Z. macroura*, from which it differs chiefly by its much shorter tail and smaller bill; its habits seem almost identical (Mayr and Short, 1970; Goodwin, 1967; personal observ.).

Ecology. Mainly forages terrestrially, and occupies open country, woodlands, and clearings within and edges around forests. Nests either arboreally or on ground. Partly migratory.

Distribution and variation. South America and adjacent (southern) West Indies. Found throughout South America north of Patagonia and southern Chile, and higher areas of the Andes Mountains. *Zenaida auriculata chrysauchenia* occurs throughout the chaco and beyond it in all directions, W to the higher Andes, N to eastern Bolivia and northern Mato Grosso, NE to Rio de Janeiro, E to the Atlantic Coast, and S to Río Negro. Races of this species are poorly defined, based on minor color differences.

Columbina squammata
Scaly Ground Dove

Taxonomy. Polytypic. Includes Middle and North American *C. "inca"* of many authors,

from which it differs chiefly in being more melanitic (more heavily barred) and in having a small white wing mark. These forms at least comprise a superspecies (Goodwin, 1967); I consider them more closely related, i.e., conspecific. This species seems to me more closely related to *Columbina* than are *Claravis* and *Metriopelia* (Goodwin, 1967), and, I would rather merge "*Scardafella*" in *Columbina* than maintain it as a weak, monotypic genus.

Ecology. A savanna and xeric woodland and desert scrub species. Lays two eggs in nest in bush or tree. Forages for seeds mainly on ground. Nonmigratory.

Distribution and variation. Occurs from arid southwestern North America discontinuously to eastern Paraguay and Misiones, Argentina. The *inca* group inhabits North and Middle America, whereas the *squammata* group occurs disjunctly in the llanos and xeric coastal areas of northern Colombia and Venezuela (of uncertain status in French Guiana), and S of Amazonia in the caatinga, campo, and eastern chaco regions (Ceará SW to eastern Bolivia, the eastern Paraguayan chaco, and Misiones). The southern population represents *C. s. squammata*, which differs from northern South American *ridgwayi* in having narrower black edges of the feathers (approaching *inca* group), and perhaps to some extent vocally (Goodwin, 1967). *Columbina squammata squammata* occurs eastward from the moist northeastern chaco (Santa Cruz, eastern Paraguayan chaco, chaco of Mato Grosso).

Columbina minuta
Plain-breasted Ground-dove

Taxonomy. Polytypic. Related rather closely to *C. passerina*, with which it occurs sympatrically.

Ecology. Terrestrially feeding woodland-edge, scrub, and savanna species. Nests in bush or on ground. Nonmigratory.

Distribution and variation. Middle America and South America, discontinuously. The several races are rather weakly differentiated (slight color differences). *Columbina minuta minuta* occupies the South American range of the species, except for northwestern Colombia. It occurs disjunctly in: (1) southeastern Venezuela and the

Guianas; (2) northwestern Peruvian coast and certain dry valleys of eastern Peru; and (3) from Maranhão and Ceará through the caatinga and campo areas to the northeastern chaco (eastern Paraguayan chaco, Mato Grosso, and thence NE). It is thus restricted to the wet, warm portion of the chaco.

Columbina talpacoti
Ruddy Ground-dove

Taxonomy. Polytypic. I include *buckleyi* of western Ecuador and northwestern Peru, regarded as specifically distinct (comprising a superspecies) by Goodwin (1967). *Columbina talpacoti* and *buckleyi* have a similar bill, larger and heavier than that of the related *C. minuta*, from which they also differ in their black rather than rufous under-wing lining. Very like the *talpacoti* group, *C. t. buckleyi* is tan rather than cinnamon and has a somewhat longer bill; otherwise these forms are very similar.

Ecology. Nests in trees or bushes, forages on the ground in diverse habitats ranging from forest clearings and cut-over areas, through savannas to scrub-desert regions.

Distribution and variation. New World, Middle America to Uruguay and northern Argentina. Disjunctly distributed in South America. The Middle American form occurs in western Colombia, and in northeastern Colombia and northern Venezuela. As noted above *C. t. buckleyi* is found in western Ecuador and Peru. *Columbina talpacoti* inhabits the Guianas, southeastern Colombia and eastern Peru, Amazonian Brazil, southern Brazil generally, S to eastern Bolivia, Paraguay, Salta, Chaco, and Corrientes, Argentina, and the northern fringe of Uruguay. This subspecies occurs in all of the chaco except the southern, ecotonal fringe of the pampas and southern chaco scrub; the chaco forms the southwestern part of the subspecies', and species', range.

Columbina picui
Picui Ground-dove

Taxonomy. Polytypic. Among the ground doves *C. picui* and *C. cruziana* (southwestern Ecuador, Peru in Marañon Valley and west coast S to the northern edge of Chile) seem to form a

closely related pair, regarded as geographic representatives by Goodwin (1967). Although generally similar to *picui*, *cruziana* differs in its heavier bill, its shorter tail, and in the lack of the white wing mark of *picui*.

Ecology. Forages on the ground, nests in bushes, favoring semi-open country or grasslands. Found at the borders of forests, in various dry or scrub woodlands, savannas, and pampas. Partly migratory.

Distribution and variation. Species and super-species endemic to South America. *Columbina picui* inhabits eastern and southern Brazil (S from southern Amazonia and the mouth of the Amazon), eastern Bolivia, Paraguay, Uruguay, northern Argentina, and central Chile. Within this range the southern of two subspecies, *C. p. picui*, occurs from southern Goiás, Mato Grosso, and southern Bahia southward. This race is found throughout the chaco, even in the driest portions. It extends beyond the chaco in all directions, although only slightly westward. This subspecies is darker, less fawn colored on the throat, less gray and "pearly" below, and browner on the back than is the northern form.

Claravis pretiosa
Blue Ground-dove

Taxonomy. Monotypic species. Distinct within its genus (Goodwin, 1967).

Ecology. Inhabits edges and forest clearings, open woodlands, and savannas. Forages on the ground, and lays two eggs in a tree nest.

Distribution. Most of Middle America and South America S to northern Peru in the W, and to northwestern Argentina, Paraguay, and Rio Grande do Sul in the E. It occurs in the northern chaco (most of the Paraguayan chaco, Santa Cruz, Mato Grosso) and in the fringes of the western Argentine chaco (Salta, Tucumán). Beyond the chaco to the W it inhabits the subtropical forest region, and it extends N and E through the range of the species.

Leptotila verreauxi
White-tipped Dove

Taxonomy. Polytypic. Forms a superspecies with central Andean *L. megalura*, from which it

differs in its slightly smaller size, less white throat and face, gray-green rather than bronze neck sheen, and paler underparts. The two overlap to some extent in northwestern Argentina and southeastern Bolivia, but *megalura* favors alder woods and forests and woodlands at a higher altitude than *verreauxi*, so the overlap is less than it superficially seems to be.

Ecology. Frequents forest and xeric woodland, feeding on the ground near trees or shrubs. Nonmigratory. Nests in trees.

Distribution and variation. Throughout lowland Middle and South America, S to northern Peru westwardly, and in the E to Mendoza and Buenos Aires, and to Uruguay (apparently absent from western areas of eastern Peru and northern Bolivia). The Middle American *verreauxi* group is represented in northern Colombia and northern Venezuela. From the Orinoco River and southern Colombia southward the *decipiens* group replaces it (see Meyer de Schauensee, 1966). *Leptotila verreauxi decipiens* occurs from southern Amazonia, Mato Grosso and Bahía S through eastern Bolivia and Paraguay to Mendoza, Argentina. This form, weakly differentiated (slightly larger than more northern races) from subspecies just to the north, meets *L. megalura* in the eastern edge of the subtropical dry forest of the Andes (where it favors drier, chaco-like situations), and it apparently intergrades in Corrientes, eastern Paraguay, and São Paulo with the distinctive (much larger and darker, resembling northwestern South American *decolor*) *L. v. chlorauchenia* of Buenos Aires and Entre Ríos, Uruguay, and southeastern Brazil. *Leptotila verreauxi decipiens* inhabits the entire chaco, frequenting brushy, denser vegetation. It extends beyond the chaco to the N, slightly to the W (see above), to the E (see above), and SW to Mendoza and San Luis.

FAMILY PSITTACIDAE

Ara ararauna

Blue and Yellow Macaw

Taxonomy. Polytypic, distinct within *Ara*. Includes *A. "caninde."*

Ecology. A large parrot frequenting forests, forest edges, savannas, and scrub. Nests in holes

in trees, laying two eggs. Social, flocking frequently. Nonmigratory.

Distribution and variation. Essentially South American, from eastern Panama and northern Colombia through most of the lowlands E of the Andes (not northeastern Venezuela) to São Paulo, Paraguay, and possibly also the northern fringe of Argentina. *Ara ararauna caninde*, considered by some a species, and apparently very rare, occurs in Paraguay and perhaps adjacent Argentina. It differs from nominate *ararauna* in having a blue rather than green forehead, and in having a green upper throat and green feathers in lines on the face. This form, possibly a morph, is treated here as a subspecies of *ararauna*. Like *Anodorhynchus glaucus*, another large macaw, it originally may have inhabited the gallery forests of the Paraguay, Parana, and Uruguay rivers, foraging into the surrounding country. These forests have been eliminated, or selectively cut-over to such an extent that the macaws largely have disappeared. Hence the status of *caninde* as a chaco form is uncertain; it may exist in small numbers along the Paraguay River, and perhaps in the western fringes of the chaco. *Ara ararauna ararauna* inhabits the chaco of Santa Cruz and Mato Grosso (pantanal).

Ara chloroptera

Red and Green Macaw

Taxonomy. Monotypic; perhaps closely related to *A. macao*.

Ecology. Inhabits forest, forest-edge, and savanna, requiring large trees for nesting. Excavates or partly excavates a cavity in which its two eggs are laid. Wanders in groups, foraging in trees for fruits and nuts.

Distribution. Mainly South American, from eastern Panama through northern Colombia, and then in a ring about Amazonia from Venezuela, Guyana, and Surinam through eastern Colombia, eastern Peru, and northern Bolivia to Paraguay, Formosa, possibly Misiones, and NE to southern Para and Bahía. Occurs in the northern chaco (of Bolivia, Mato Grosso, northern and eastern chaco of Paraguay, and Formosa), mainly in the wetter eastern region. Birds reported from the lower Paraguay River (Formosa, southern Paraguay) may be wanderers from the north.

Ara auricollis
Golden-collared Macaw
Figure 26

Taxonomy. Monotypic. Forms a superspecies with *A. maracana* of the campo, caatinga, and highland Brazilian forest, and *A. couloni* of eastern Peru. These species have an identical tail pattern; they are similar in size, with similar back color and wing color (all lack red, yellow or orange in the wings). *Ara maracana*, which narrowly overlaps *auricollis* in western Mato Grosso and northeastern Paraguay, differs from the latter in having red on the belly, back, and forehead, in lacking a yellow nape patch, and in its mainly blue (not black) crown. *Ara couloni* resembles *auricollis*, but has blue over much of

its head, black is restricted to the forecrown, and its face is more fully feathered; it lacks the yellow nape of *auricollis*.

Ecology. A woodland, forest-edge, and savanna macaw, nesting in holes in trees (lays four eggs; Olrog, 1968). Nonmigratory. Social.

Distribution. Superspecies endemic to central South America. *Ara auricollis* is found in northern and eastern Bolivia, northwestern Argentina (Jujuy, Salta), northern Paraguay mainly W of the Paraguay River, and southwestern Mato Grosso. Inhabits the northern chaco in the pantanal of Mato Grosso and Paraguay, the northern Paraguayan chaco, Santa Cruz, and perhaps the west-central fringes of the chaco in northwestern Argentina. Extends W from the chaco into the subtropical dry forest, and to the N and NW.

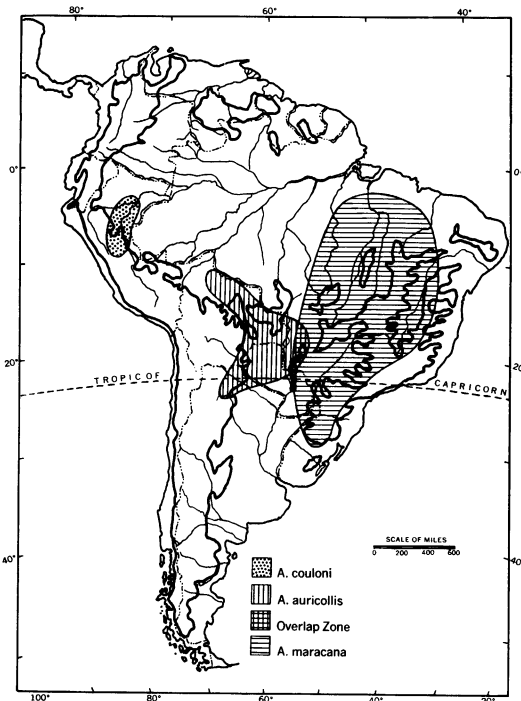


FIG. 26. Range of superspecies *Ara maracana*, including *A. couloni* and chaco-dwelling Golden-collared Macaw, *A. auricollis*. Allospecies of *auricollis* occur in seasonally dry forest of east-central Peru, and in campo-caatinga region. *Ara auricollis* occupies chaco-Amazonian forest ecotone and adjacent portions of northern chaco, dry subtropical forest, and Amazonian Bolivia.

Aratinga acuticauda
Blue-crowned Parakeet
Figure 27

Taxonomy. Polytypic. Relationships in its genus not certain.

Ecology. A flocking species, like most parakeets. Inhabits dry woodlands, savannas, caatinga, and even pampas. Nests in holes in trees.

Distribution and variation. Endemic in South America in three disjunct populations, which are moderately differentiated. These are: (1) *neoxena* in northeastern Colombia and northwestern Venezuela; (2) *hemorrhous* in the caatinga (Piauí, Bahia); and (3) *acuticauda* from northern Bolivia and western Mato Grosso S through Paraguay to San Juan, La Pampa and (northern) Buenos Aires (occurs E to Misiones, southwestern Rio Grande do Sul, western Uruguay; and W to the foothills of the Andes). The last race occurs throughout the chaco, and beyond it in all directions; it is larger than the other races, and its head is bluer.

Aratinga leucophthalmus
White-eyed Parakeet

Taxonomy. Polytypic. This parakeet forms a superspecies with *A. finschi* of Middle America (they have been treated as conspecific; Meyer de Schauensee, 1966). Both species are similar in

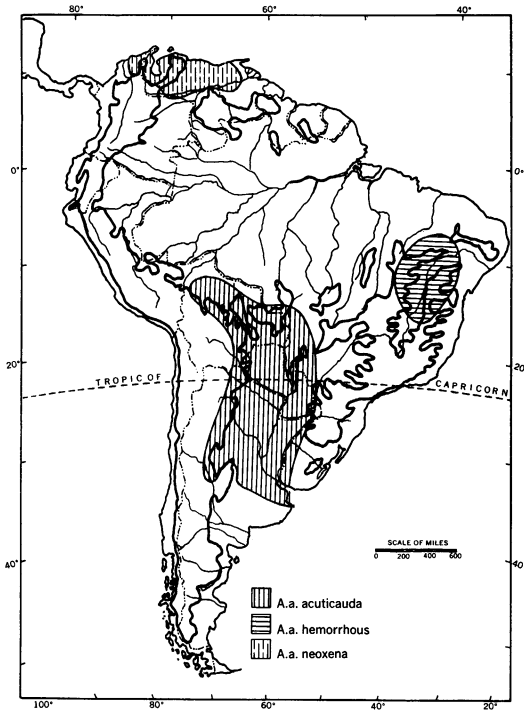


FIG. 27. Range of Blue-crowned Parakeet (*Aratinga acuticauda*). Disjunct races occur in generally dry northern areas, caatinga, and chaco-pampas-subtropical dry forest.

bill shape, in the red (orange, yellow) under the wing, and generally in coloration including the lack of red on the thighs. *Aratinga leucophthalmus* is somewhat larger than *finschi*, and is variable in having a sprinkling of red about its body plumage; *finschi* has red restricted to a patch on the forehead.

Ecology. Inhabits diverse forests and woodlands and gallery forests in savannas. Flocks much of the time.

Distribution and variation. Endemic in South America. Occurs in lowlands from eastern Colombia, southeastern Venezuela, and the Guianas S through Brazil, eastern Peru, and eastern Ecuador, northern and eastern Bolivia to Catamarca and Santa Fe, Argentina, and northern Uruguay. *Aratinga leucophthalmus leucophthalmus* inhabits all of this range except the northwestern portion; it is larger, paler green, and lacks the often extensive facial red of the

northwestern forms (it also tends to have less red along the leading edge of the wing). *Aratinga leucophthalmus leucophthalmus* occurs throughout the chaco, and beyond it to the W (slightly), the E (to the Atlantic Ocean), and to the N.

Aratinga aurea
Peach-fronted Parakeet

Taxonomy. Polytypic. Comprises a superspecies with Middle American *canicularis*, which closely resembles *aurea* but shows more blue in the crown and tail, has a pale rather than black bill, and in place of the gold orbital feathering of *aurea*, it instead has a larger bare (skin) area around the orbit.

Ecology. Another parakeet that bands in large flocks, inhabiting forest edges, open woodlands, savanna, and pantanal. Little known.

Distribution and variation. Endemic in central-eastern South America from the Amazon S through all of Brazil to Rio Grande do Sul, eastern (and northern) Bolivia, western Paraguay (also northern fringe of eastern Paraguay), and northern Salta and eastern Formosa, Argentina. There are two distinct intergrading races, including *A. a. major*, which is considerably larger, and greener (darker green), with a yellower, less gold forehead patch than nominate *aurea*. *Aratinga aurea major* inhabits the northern chaco, to which it is essentially confined. It occurs in the chaco of Santa Cruz, Mato Grosso, western Paraguay, and northern Salta. *Aratinga aurea aurea* apparently enters eastern Paraguay from Mato Grosso, and apparently it occurs in the pantanal along the Paraguay River of central Paraguay S to eastern Formosa (Olrog, 1963).

Aratinga nenday
Black-hooded Parakeet

Taxonomy. Monotypic (see Meyer de Schauensee, 1966). This species, usually treated as comprising a monotypic genus *Nandayus*, seems congeneric with *Aratinga*. Its generic features include a rather long tail, small bill, and black crown; however close resemblance in pattern, general external morphology, and habits indicate that it can be included readily in *Aratinga*

and does not merit generic separation (as a monotypic genus).

Ecology. Frequents pantanal, ranging into the chaco and adjacent campos. Frequents palms, in which it nests. Congregates in vast flocks, which may wander widely, especially in the nonbreeding season.

Distribution. Endemic in the pantanal and adjacent regions of central South America. It is found from Santa Cruz and southwestern Mato Grosso through central Paraguay to northern Santa Fe, Argentina. It occupies the entire pantanal portion of the eastern chaco and extends into the central chaco, perhaps only for foraging or seasonally.

Pyrrhura molinae
Green-cheeked Parakeet

Taxonomy. Weakly polytypic. Relationships are difficult to establish within this genus; its close relatives may include *P. frontalis*. Included within *P. molinae* is *P. "hypoxantha,"* which I consider to represent xanthomorphic variants of *molinae*. Only a few specimens of this form are known, they come from areas (in Mato Grosso) where *molinae* occurs, and they resemble (specimens examined) *molinae* in features other than those apt to be affected by overdeposition of yellow (and whitish-yellow) and red pigment.

Ecology. Not well known. Frequents forest, including dry subtropical forests, savannas, and the fringe of the chaco. Occurs in large flocks.

Distribution and variation. Endemic in northern and eastern Bolivia, western Mato Grosso, and Salta and Jujuy, Argentina. Inhabits the fringes of the chaco in Santa Cruz, Bolivia, possibly the northern and western edges of western Paraguay, and the subtropical dry forest-chaco ecotone of Salta. A specimen (in the United States National Museum) was collected by the Capt. T. J. Page expedition in "Paraguay," possibly along the Paraguay River in northern Paraguay. Color differences among the three races involve the paler or darker blue in the wings, the color of the crown, and the tail. All three subspecies could occur in the chaco, *phoenicurus* in Mato Grosso, *molinae* in Bolivia, and the paler *australis* in Salta.

Pyrrhura frontalis
Reddish-bellied Parakeet and
Pyrrhura devillei
Blaze-winged Parakeet
Figure 28

Taxonomy. Polytypic. These form a super-species, although it is possible, even likely, that they are conspecific. *Pyrrhura devillei* is virtually identical to the adjacent *P. frontalis chiripepe*, except for having red, or red-orange and yellow under the leading edge of the wing. These interbreed at least sporadically in northern Paraguay (Short, in prep.); it is possible that *devillei* is a geographical morph of *frontalis*.

Ecology. These species occur in woodlands,

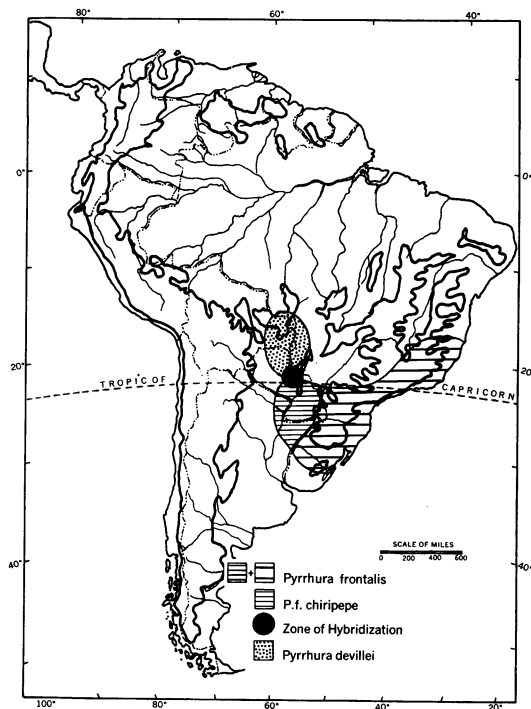


FIG. 28. Range of Reddish-bellied Parakeet (*Pyrrhura frontalis*) and Blaze-winged Parakeet (*P. devillei*). Latter ecotonal (chaco-campo-Amazonian forest) species, if indeed specifically distinct, interbreeds at least sporadically with *P. frontalis* where shown on map. *Pyrrhura frontalis* is southeastern Brazilian forest species that extends westward through the ecotone and into eastern chaco.

forests, forest clearings, and pantanal. They move about in flocks, foraging mainly for fruits and nuts.

Distribution and variation. The superspecies is endemic to east-central South America. *Pyrhura devillei* is confined to the northeastern Paraguayan chaco, Santa Cruz, and southwestern Mato Grosso. *Pyrhura frontalis* replaces it south-eastward, ranging from the northern Paraguayan pantanal, eastern Formosa, and eastern Chaco through eastern Paraguay and Corrientes to the Atlantic Coast from Bahia to northern Uruguay. Moderately differentiated *P. f. chiripepe* inhabits the western range of the species in central and eastern Paraguay, eastern Formosa, eastern Chaco, and Corrientes. It is paler, possibly slightly smaller, and with bluer, less violet primaries than races to the E. *Pyrhura devillei* is almost confined to the northeastern chaco in wooded areas of the pantanal and along rivers, but probably forages well into the eastern chaco woodland. *Pyrhura frontalis chiripepe* within the chaco seems confined to the vicinity of riparian forests along the Paraguay River and adjacent large chaco rivers emptying into it, but this form also may range into surrounding areas of chaco woodland, as well as the southern pantanal.

Myiopsitta monachus
Monk Parakeet

Taxonomy. Polytypic species, monotypic genus. No close relatives.

Ecology. An open country and dry woodland parakeet, requiring only sparse tree cover for nesting. Nests communally in large stick nests, which may be used for roosting after the breeding season.

Distribution and variation. Endemic in South America, occurring from eastern (perhaps northern) Bolivia and southwestern Mato Grosso S through Paraguay and Argentina to Rio Grande do Sul, Uruguay, and the northern fringe of Patagonia. Four subspecies are recognized; *M. m. luchi* of the subtropical zone of central Bolivia is distinct, with its yellow belly and pale underwings, and *M. m. monachus* of Santa Fe and Entre Ríos to southern Buenos Aires (very large,

pale blue in wings) is moderately differentiated. The other races, *catita* and *cotorra* are weakly characterized, but both are smaller than *monachus* with bluer wings. *Myiopsitta monachus catita* occupies the southern chaco from Paraguay and Tarija, Bolivia, southward, extending beyond the chaco to La Pampa and Río Negro. It is replaced in the northern and eastern chaco by *M. m. cotorra*, which ranges from the Bolivian chaco, the pantanal of Mato Grosso, and the Paraguayan chaco S along the Paraguay-Parana rivers to Santa Fe, and E to Mato Grosso, Misiones, and Rio Grande do Sul.

Forpus xanthopterygius
Blue-winged Parrotlet

Taxonomy. Polytypic. Forms a superspecies with *F. passerinus* (lower Amazon, Colombia to Guianas) with which it often is merged. Essentially *passerinus* (males) is green-rumped or blue-green rumped, and *xanthopterygius* is blue-rumped; they may indeed be conspecific, but have been taken close together along the Amazon with no sign of interbreeding.

Ecology. Little-known, frequents forests, forest edges, and scrub woodland, forages in open areas (even on ground) adjacent to forests.

Distribution and variation. The superspecies is endemic to South America. *Forpus xanthopterygius* occurs disjunctly in northern Colombia, in western Amazonia (Peru, Colombia, Brazil), northern and eastern Bolivia, and eastern Brazil from Ceará and Pernambuco to Rio Grande do Sul, extending into eastern Paraguay and Corrientes and Misiones, Argentina. It may occur in the chaco, along the Paraguay River (Formosa, southern Paraguay), and possibly in Santa Cruz, Bolivia. Birds breeding in eastern Paraguay may forage in the area immediately adjacent to the Paraguay River along its western Bank. The race *xanthopterygius* is that most likely to be found in the chaco, occurring through the greater part of the eastern disjunct range noted above except Ceará and Piauí. It is distinguished from the adjacent race (*flavissimus*) of the latter states by the lack of violet in the rump of males, and by the lack of yellow in the forehead.

Brotogeris versicolurus
Canary-winged Parakeet

Taxonomy. Polytypic. Relationships in *Brotogeris* are unclear.

Ecology. A forest and savanna species, nesting in trees and foraging in flocks. Possibly migratory to some extent (southern race).

Distribution and variation. Endemic in South America. Found from French Guiana and the Amazon Valley W to southeastern Colombia, Ecuador, and Peru, and in an arc SE through northern and eastern Bolivia, Mato Grosso, and eastern Brazil to interior Ceará; S from Bolivia and Mato Grosso to Salta, eastern Chaco, and Misiones, Argentina. Apparently it is lacking in southern Amazonia. Of the three distinct races, *B. v. behni* of central Bolivia to Salta occurs in the western edge of the chaco (Salta, probably far western Paraguay), and *B. v. chiriri* occupies a range from northwestern Bolivia to eastern Brazil, including Santa Cruz, Bolivia, the chaco of Mato Grosso, and the Paraguay River to its mouth. The latter race thus occurs in the pantanal region and perhaps the eastern moist chaco woodland. It is doubtful if the two races meet in western Paraguay, although some seasonal movement may occur into that region. *Brotogeris versicolurus chiriri*, like nominate *versicolurus* to the N, is small, but it lacks a white patch in the wing and is paler yellow-green. *Brotogeris versicolurus behni* is large; it too lacks white in the wing and is dull blue-green in general color.

Pionus maximiliani
Scaly-headed Parrot

Taxonomy. Polytypic. Relationships not established with other congeneric species, but does not seem especially close to any.

Ecology. Inhabits forest and xeric woodland, nests in trees, and occurs in flocks.

Distribution and variation. Endemic in central South America. Inhabits the caatinga, the chaco, and southern Brazilian forests (eastern Bolivia and northern Argentina to the Atlantic Coast from Bahía to Rio Grande do Sul). It is doubtful if the species breeds in the dry central Argentine chaco, but it is otherwise found throughout the chaco. Subspecies found in the

chaco include the closely similar *siy* and (probably) *lacerus*. The latter occurs in Tucumán, adjacent Salta, and Catamarca; it differs from *siy* in its heavier bill and more purple breast. *Pionus maximiliani siy* occurs mainly in the chaco, from the range of *lacerus* N in the subtropical dry forest along the Andes to central Bolivia, E across the Paraguayan chaco and Santa Cruz to western Mato Grosso, and S in the eastern chaco to northern Santa Fe. It intergrades with other races to the east (see Smith, 1960). Both *siy* and *lacerus* differ from the other two races of *maximiliani* in their darker ventral color, their purpler (less blue) breast, which seems to vary clinally, and in their yellower back color.

Amazona aestiva
Turquoise-fronted Parrot

Taxonomy. Polytypic. Forms a superspecies with Middle American to Amazonian *A. ochrocephala* and probably *A. barbadensis* of coastal Venezuela and islands off its coast. These very similar, allopatric species have yellow or red "wrist" areas (except one race of *ochrocephala*), usually they have yellow thighs, and black bars are well developed in the body plumage. *Amazona aestiva* differs from the other species in its black bill, in having blue-green in the facial yellow, and in much red under its wings. *Amazona ochrocephala* has a fully yellow head, somewhat less black barring on its body, and a pale or black bill; it too has much red in the wings. *Amazona barbadensis* may have a yellow head, or the yellow may be reduced (forehead or nape only), its wings show less red than in the other two species, its bill is pale, and it is smaller.

Ecology. A large, loud forest and woodland (including chaco) species usually occurring in pairs, or small groups, nesting in trees, and feeding entirely in trees.

Distribution and variation. Endemic in central south America, from northeastern Bolivia and Piauí S to Tucumán and Rio Grande do Sul. Weakly defined eastern and western races are recognized, the western *xanthopteryx* differing from nominate *aestiva* in its generally yellower, that is orange or yellow-orange, wrist patch, rather than having the red patch of *aestiva* (which

varies somewhat in this feature). The subspecies, *xanthopteryx* occurs throughout the chaco, slightly beyond it to the W (foothills of the Andes) and N (northern Bolivia, central Mato Grosso), and E to central Mato Grosso, eastern Paraguay and Misiones, intergrading there with *aestiva*.

FAMILY CUCULIDAE

Coccyzus cinereus
Ash-colored Cuckoo
Figure 29

Taxonomy. Monotypic. Closely related to Colombian and Venezuelan *C. pumilus*, with which it forms a superspecies. These species are distinguished from other species of *Coccyzus* by their small size and color patterns. *Coccyzus pumilus* is smaller than *C. cinereus*, and it has a rufous throat, but these species otherwise are similar in pattern, and their bills are very much alike.

Ecology. Inhabits dry woodlands, savannas, and pampas, frequenting brushlands and scattered wooded areas in the pampas. Nonparasitic, laying two or three eggs in a stick nest in a bush or tree. Possibly migratory in extreme S.

Distribution. The superspecies is endemic in South America. *Coccyzus cinereus* is found from northern and eastern Bolivia S through western and most of eastern Paraguay, and Argentina S to La Pampa and southern Buenos Aires. It reaches the subtropical dry forest along the Andes in the W, and Misiones and western Uruguay (probably southwestern Rio Grande do Sul) in the E. Additionally, disjunct populations may occur in Bahía and Goiás, but records from there may be of migrants from southern Argentina, where it is unlikely that this cuckoo winters. It inhabits all of the chaco, and extends beyond it in all directions.

Coccyzus melacoryphus
Dark-billed Cuckoo

Taxonomy. Monotypic. Comprises a superspecies with the larger, grayer-backed, and partly yellow-billed *C. minor*, a mainly mangrove-inhabiting species of Middle America and the West Indies (adjacent Florida, islands off north-

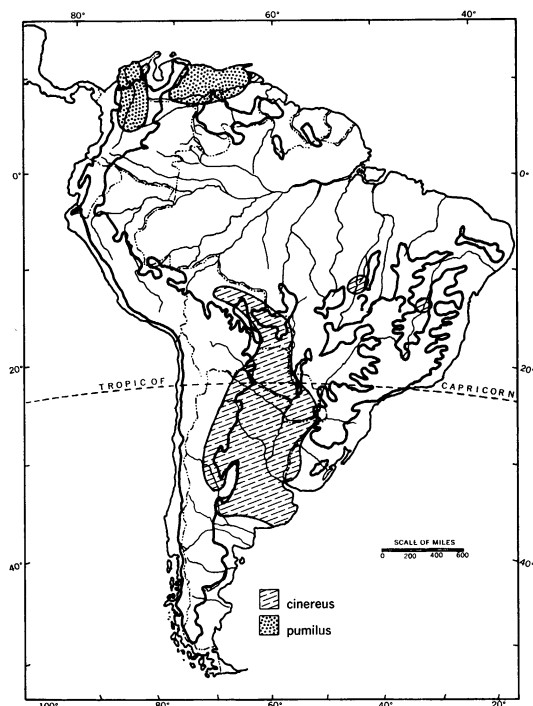


FIG. 29. Range of superspecies *Coccyzus cinereus*, including *C. pumilus* (two arid zone isolates in northern South America) and Ash-colored Cuckoo (*C. cinereus*). Latter occupies chaco, pampas, chaco scrub, and dry subtropical forest; disjunctions shown may represent migrant birds and not breeding populations (see text).

ern South America as well) and coastal northeastern Venezuela, parts of the Guianas, and Brazil to the mouth of the Amazon. It is sympatric with *melacoryphus* in the latter areas and on Trinidad, but considerable ecological isolation probably occurs.

Ecology. Frequents forest, woodland, and open country in brushy areas. Nests in trees or bushes.

Distribution. South America, Galapagos Islands, and Trinidad. On the continent occurs from west-central and northern Peru N to Colombia and throughout the lowlands E of the Andes, except for southeastern Venezuela and adjacent Guyana, S to San Juan and central Buenos Aires. It occurs in denser vegetation throughout the chaco and beyond it in all directions.

Piaya cayana
Squirrel Cuckoo

Taxonomy. Polytypic. Sympatric with its several congeneric relatives.

Ecology. Frequents forest and savanna regions, skulking through dense tangles of vegetation. Nests in trees, and is not parasitic. Nonmigratory.

Distribution and variation. New World, Mexico to northwestern Peru and, in the E, to parts of northern Argentina and northern Uruguay. Within South America it occurs from northwestern Peru to northern Colombia, and then E and S throughout eastern South America to Tucumán in western Argentina, Santa Fe and Entre Ríos in eastern Argentina, and Uruguay. The species occurs in all of the chaco except the dry central Argentine portion, and to the W, N, and E of the chaco. All but the northern and western extremes of its chaco range are inhabited by the very distinctive *P. c. macroura*, with its chestnut back, fawn-colored throat and very black belly and tail. This race, which occurs from the Paraguayan chaco E to southern Bahía and thence S through the southeastern part of the species' range, resembles northern South American races rather than those surrounding it. The southwestern edge of the chaco is reached by *P. c. mogenseni*, which occupies the subtropical dry forest of northwestern Argentina and southern Bolivia. In the northern chaco (northernmost western Paraguay, Santa Cruz, Bolivia), and most of the (northern) Mato Grosso pantanal occurs *P. c. cabanisi*; it extends from central Bolivia through Mato Grosso to Bahía directly N of *macroura*. The races *cabanisi* and *mogenseni* differ from *macroura*, which they surround, in their rufous (not chestnut) coloration and rusty throat. *Piaya cayana cabanisi* is paler below and whiter, with the ventral black almost totally replaced by gray, whereas *mogenseni* is darker gray below, and shows more black on the belly.

Crotophaga major
Great Ani

Taxonomy. Monotypic. Not especially closely related to either of the smaller species of ani.

Ecology. Social, frequents dense vegetation of all types (swamps, forest edges, and clearings, second-growth, and river-edge tangles) in forests and savannas. Several females place their eggs in a single nest. Not parasitic or migratory. Feeds on diverse insects and fruits.

Distribution. Mainly South America, from Panama to northern Colombia, and then E and S throughout the lowlands to Salta, eastern Formosa, Santa Fe, and northern Uruguay. It occurs in the chaco from Salta and western Paraguay to Santa Cruz, and in the E throughout the pantanal and eastern chaco to Santa Fe. From the chaco it extends slightly W (subtropical dry forest), N, and E.

Crotophaga ani
Smooth-billed Ani

Taxonomy. Monotypic, sympatric with other anis.

Ecology. Frequents forest edges, clearings, cultivated lands, savannas, and brushlands, occurs in small to large groups. Nonmigratory, but wanders about in bands. Constructs its own nest.

Distribution. Southern North America S to Ecuador, and in the eastern South American lowlands to La Rioja, Santa Fe, and northern Uruguay. It reaches the southern edge of its range in the chaco-pampas ecotone. This ani is found sporadically throughout the chaco, and to the W, N, and E.

Guira guira
Guira Cuckoo

Taxonomy. Monotypic genus and species, with no close relatives.

Ecology. This distinctive, highly social cuckoo ranges through bushy areas, favoring semi-open country, but on occasion found also on pampas far from trees or bush. Several females place what look to be decorated eggs (blue with raised areas of chalklike, white "scribbling") in a single nest in a tree.

Distribution. Endemic to eastern and central South America, from the mouth of the Amazon through campo, caatinga, and forested southeastern Brazil to eastern Bolivia, Mendoza, and Río Negro, Argentina. It occurs throughout the chaco and beyond it in all directions.

Tapera naevia
Striped Cuckoo

Taxonomy. Polytypic species, monotypic genus.

Ecology. Inhabits woodland and brushland in both open country and forests. Solitary in habit, it parasitizes small birds, laying its eggs in their nests.

Distribution and variation. New World in Middle and South America. Found in western South America from Ecuador northward, and in the E throughout the lowlands to La Rioja and Buenos Aires, Argentina. Three moderately differentiated races occur, including *T. n. chochi* from northern Bolivia, southern Amazonia and Maranhão S through eastern and central Brazil, Paraguay, and Uruguay to central Argentina. This form is larger than northern subspecies, it has pale spots on the crown (lacking in others), and it is browner, with a brown rump, and buffier in tone than in nominate *naevia*. The race *chochi* is found throughout the chaco and beyond it in all directions.

Dromococcyx pavoninus
Pavonine Cuckoo

Taxonomy. Polytypic, sympatric with its congener *phasianellus*.

Ecology. Medium-sized, skulking, and parasitic. Nonmigratory.

Distribution and variation. Endemic in South America. Discontinuously distributed (uncommon, or so shy and retiring that it appears uncommon, but it may be overlooked by collectors) in northwestern and north-central Venezuela, in parts of the Guianas W to southern Venezuela, eastern Ecuador, and western Amazonian Brazil and Peru, and from eastern Bolivia, central Paraguay, and Misiones NE to Goiás and Rio de Janeiro. The southern disjunct range is occupied by the weakly differentiated (chiefly small size) *D. p. pavoninus*. This form is known from the chaco in the Paraguayan chaco, Santa Cruz, and the pantanal region of Mato Grosso.

FAMILY TYTONIDAE

Tyto alba
Barn Owl

Taxonomy. Strongly polytypic. Forms a

superspecies with *T. rosenbergii* (Celebes; see Mayr and Short, 1970).

Ecology. Frequents buildings and other edifices, and nests there. Usually forages in fairly open, or open country, at night, and mainly preys on rodents.

Distribution and variation. Cosmopolitan, in New World throughout all regions of both continents, although commonest near human habitations. It occurs at least sporadically throughout the chaco. The many races vary considerably in their levels of differentiation. *Tyto alba tuidara* of the chaco, and of all South America S of the Amazon River and northwestern Bolivia, is a trifle paler than races to the N.

FAMILY STRIGIDAE

Otus choliba
Tropical Screech Owl

Taxonomy. Polytypic, forming a superspecies with the blacker, more heavily marked *O. robortus* of western Peru (they are perhaps conspecific, Meyer de Schauensee, 1966).

Ecology. Common, frequents lowland forest, woodland, and brushland, nests in tree cavities. Nonmigratory.

Distribution and variation. New World, from Costa Rica to northern Columbia, then E and S to San Luis and northern Buenos Aires, Argentina, and to Uruguay. Many races of varying distinctiveness are recognized. The southernmost subspecies, *O. c. choliba*, occurs from eastern Bolivia, southern Mato Grosso and São Paulo S through the subtropical dry forest and scrub (monte) along the base of the Andes, the chaco, southeastern Brazilian forest and pampas to San Juan, Córdoba, and Buenos Aires. This form, which occurs throughout the chaco, is one of the darker races, but is brown (not dark gray or blackish), less rufous, and less gray than others.

Bubo virginianus
Great Horned Owl

Taxonomy. Polytypic. With Old World *B. bubo* forms a superspecies.

Ecology. This large eagle-owl is very diverse in habitats occupied, from lowland forests of the tropics, where it is generally uncommon, to open grassland and desert, even at high altitudes. Terri-

torial, nonmigratory; preys on mammals and birds. Nests in trees, cliffs, or on the ground.

Distribution and variation. New World, Arctic to Tierra del Fuego. In South America it ranges throughout except for the main Amazonian region of Brazil and southern parts of the Guianas (but it is found in the lower Amazon) and the eastern tip of Brazil. The southeastern *B. v. nacurutu* occurs from northern Bolivia S along the eastern edge of the Andes to Río Negro, Argentina, and E to the Atlantic Coast (N to Bahía). This form is very finely barred below, grayish ventrally with almost no rusty, and finely vermiculated dorsally with gray and brown (adjoining races are more broadly barred, and, to the SW browner and the NW rustier in color). This subspecies ranges throughout the chaco and beyond it in all directions.

?Pulsatrix perspicillata
Spectacled Owl

Taxonomy. Polytypic, sympatric with related species.

Ecology. Frequents forest, forest edge, and savanna; its habits are little known.

Distribution and variation. Middle and South America. Occurs S to Ecuador in western South America, and in the E it reaches Tucumán in subtropical dry forest, eastern Bolivia (Santa Cruz), the northern fringe of eastern Paraguay, and Rio Grande do Sul; of questionable occurrence in the western fringes, the northern edge, and the Mato Grosso portion of the chaco. Races that may occur in the chaco are *boliviana* (large, light brown) in the western fringe and in the N, and *pulsatrix*, smaller and paler below, in the E.

Glaucidium minutissimum
Least Pygmy-owl

Taxonomy. Polytypic. Relationships are with the next species, with which it is sympatric.

Ecology. Occupies forest and woodland; little known.

Distribution and variation. New World, spottily distributed in Middle and South America. Except for Colombia adjacent to Panama, the South American range is that of *G. m. minutissimum*, a distinct race, paler, more rufous (less brown) above, and rufous rather than chestnut

below compared with Middle American forms. This subspecies apparently occurs disjunctly about the mouth of the Amazon, in the Venezuelan-Guianan highlands, in the Rio Branco region, in southern Mato Grosso and adjacent Paraguay, in western São Paulo, and in Bahía. It may extend through the intervening regions. This race apparently occurs in the northeastern Paraguayan chaco and adjacent Mato Grosso.

Glaucidium brasilianum
Ferruginous Pygmy-owl
Figure 30

Taxonomy. Polytypic. Various workers consider *G. jardinii* of montane Middle America and northern South America, and Patagonian-Chilean *nanum* conspecific with *brasilianum*, but I follow Meyer de Schauensee (1966) and Mayr and Short (1970) in treating them as species, components of a superspecies with *brasilianum*. The very dark blackish or rufous *jardinii* has more back spotting than *brasilianum*. Larger than the other species, *G. nanum* has fine bars on its tail, and its sides are partly barred; *brasilianum* is smaller with broader tail bars and unbarred sides. These and other minor differences exceed those found among races of *brasilianum*. Furthermore, the disjunct range of *jardinii* and *brasilianum* (in western Peru and Chile, implying trans-Andean crossing of a consubspecific population) suggests a complicated and historically ancient pattern of sympatry, or at least contact, which, without evidence of interbreeding, seems to imply that the forms are species.

Ecology. A diurnal predator upon insects, chiefly, and frequenting forests, woodlands, and brushland.

Distribution and variation. New World, Nearctic to Uruguay and central Argentina, *Glaucidium brasilianum brasilianum* occupies the southern range of the species, from the Amazon River, northern and eastern Bolivia, all of central and southern Brazil, S along the Andes to La Rioja, and E to the Atlantic Coast; it also occurs disjunctly in western Peru and northern Chile. This subspecies is deeper in color than more northern forms.

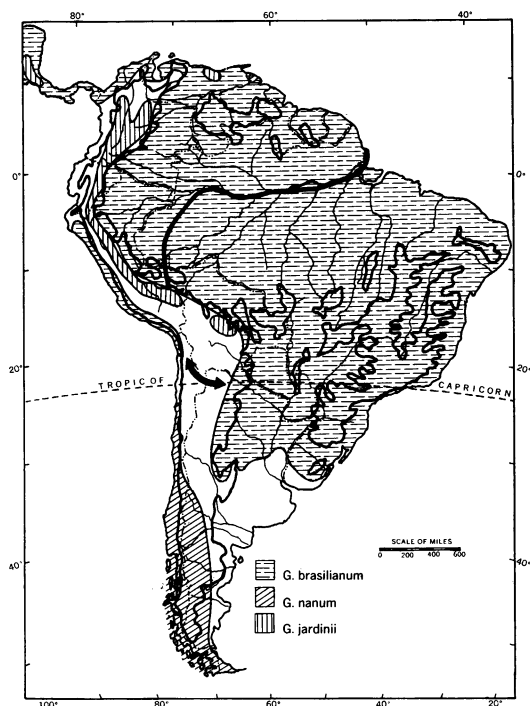


FIG. 30. Range of Ferruginous Pygmy-Owl (*Glaucidium brasilianum*) and its allospecies *G. nanum* and *G. jardinii*. *Glaucidium brasilianum* occurs in all manner of lowland forests and brushlands north to North America. Western isolate (Peru to Chile) of *brasilianum* is same subspecies as that found east of the Andes. *Glaucidium jardinii* is montane forest species with disjunct highland populations in some cases surrounded by lowland *G. brasilianum*. *Glaucidium nanum* is a Fuegian forest species, possibly conspecific with *brasilianum*.

Athene cucularia
Burrowing Owl

Taxonomy. Polytypic. The only species of *Athene* in the New World, and related to Eurasian *A. noctua* (Mayr and Short, 1970).

Ecology. Primarily insectivorous and terrestrial, found in semi-open and open country habitats. Nests in a cavity in the ground. Nonmigratory.

Distribution and variation. New World, from grasslands of Nearctic discontinuously through Middle America and West Indies to southern

Patagonia. In South America isolated populations occur in central Colombia, in northern, central, and southern Venezuela and adjacent Guyana, Brazil and Colombia, and in southern South America from western Ecuador, highland Bolivia, eastern Bolivia, Goiás, and Maranhão S to central Chile and northern Tierra del Fuego. *Athene cucularia cucularia* is the southern race, inhabiting the area S of northern Chile, eastern Bolivia, eastern Paraguay, and Rio Grande do Sul. This form, with adjacent Andean *juninensis*, attains the largest size in this species; in color, however, it is dull brown not rufous like *juninensis*, and it rather strongly resembles Peruvian *nanodes*, which seems a small version of *cucularia*. The last form is found throughout the chaco in suitably open (including cultivated) areas, and it extends beyond the chaco in all directions except N.

?*Ciccaba huhula*
Black-banded Owl

Taxonomy. Polytypic. I include Middle American *nigrolineata* (S to Ecuador and Peru disjunctly in W, and to central Colombia and northwestern Venezuela) and *huhula* in a super-species (Wetmore, 1968); they have been merged, but they may interbreed only sporadically (see Blake, 1958) and hence be separate species. *Ciccaba nigrolineata* is very similar to *huhula*, but more finely barred ventrally (hence appearing much whiter), and lacks bars on the lower back and head.

Ecology. A forest and savanna owl; nonmigratory.

Distribution and variation. Endemic in South America, replacing *nigrolineata* in southern Venezuela and southeastern Colombia. It extends from there continuously to French Guiana in the E and eastern Peru to the S, but a hiatus may occur in western Amazonian Brazil, as it does north of the Amazon E to its mouth. It is found from the Amazon S through Amazonia, Pará, and Maranhão to the dry subtropical forest along the Andes in Jujuy and Salta, eastern Bolivia, northeastern Paraguay, Misiones, and the Brazilian highlands from Santa Catarina to Minas Gerais. The portion of the last range W of central Amazonia and eastern Bolivia is occupied by *C.*

h. huhula, and the eastern portion by the distinctly larger *albomarginata*. *Ciccaba huhula huhula* probably occurs in the chaco at its western edge (in Salta perhaps), and *albomarginata* is likely to occur in the Santa Cruz and Mato Grosso chaco (possibly in the Paraguayan chaco).

Strix hylophila
Rusty-barred Owl
Figure 31

Taxonomy. Monotypic. As owls go, I do not feel that this species sufficiently resembles allopatric *rufipes*, the only other South American member of this genus, to consider them as component species of a single superspecies.

Ecology. A little-known large owl of the southeastern Brazilian wet forest.

Distribution. Endemic in southeastern Brazil and adjacent Paraguay and Argentina. Found from eastern Formosa, Misiones, and eastern Paraguay NE to Minas Gerais, E to the Atlantic Ocean, and SE to Rio Grande do Sul. It has occurred in the chaco only in eastern Formosa, and it may be expected to occur in the adjacent Paraguayan chaco.

Strix rufipes
Rufous-legged Owl
Figure 31

Taxonomy. Polytypic. Related to allopatric *hylophila*, but not so closely as to form a superspecies.

Ecology. A hole-nesting, dry woodland, and forest owl; little known.

Distribution and variation. Endemic in southern South America, where it occurs in two disjunct, well-marked populations. The northern *chacoensis* (larger, much grayer brown and less rufous) occurs from the Paraguayan chaco SW through the western chaco and dry subtropical forest, to La Rioja and La Pampa. The smaller, more rufous *rufipes* occurs in the Fuegian forests from central Chile and Neuquén S to Tierra del Fuego. *Strix rufipes chacoensis* inhabits the central and western chaco, but not the northern, warmer (Santa Cruz, northern Paraguayan chaco) chaco, nor the eastern pantanal and moist chaco woodland.

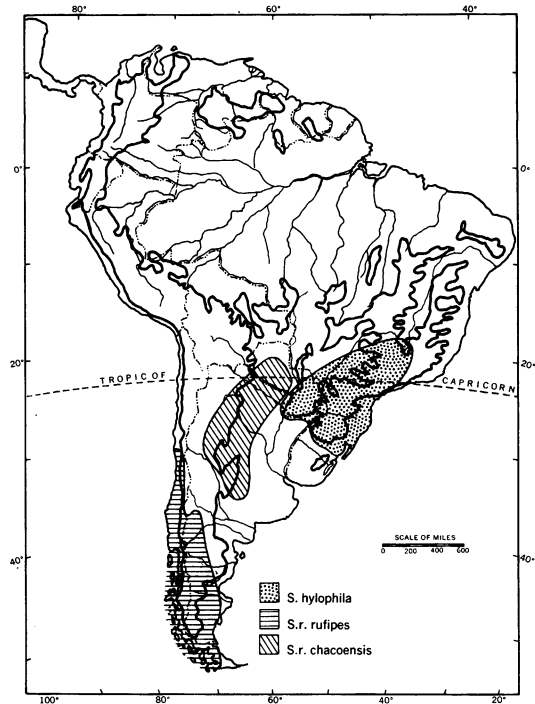


FIG. 31. Range of Rusty-barred Owl (*Strix hylophila*) and Rufous-legged Owl (*S. rufipes*). These species replace one another, *hylophila* in southeastern Brazilian forest (eastern chaco), and *rufipes* from drier chaco southwestward. They have not been taken together. Disjunct races of *rufipes* occur in Fuegian forest, and in chaco, dry subtropical forest, and part of chaco scrub.

Asio clamator
Striped Owl

Taxonomy. Polytypic. This species is certainly congeneric with *Asio*, and seems related rather closely to *A. otus* and *A. flammeus* (see Mayr and Short, 1970).

Ecology. A forest, woodland, and swamp owl, which nests on the ground and forages over grasslands and marshes (Wetmore, 1968).

Distribution and variation. Middle and South America, discontinuously. Two isolates occur in South America, one from Venezuela and the Guianas SW to eastern Peru, and the other from eastern Bolivia, Mato Grosso and Bahía S to Tucumán, northern Buenos Aires, and Uruguay. The southern isolate *A. c. midas* is much larger,

buffier, grayer and less rufous than northern races. It occurs in wetter, open areas throughout the chaco, and beyond slightly to the W, and to the N, E, and S.

Asio flammeus
Short-eared Owl

Taxonomy. Polytypic. Related to *A. capensis* of Africa (Mayr and Short, 1970; see *A. clamator*).

Ecology. Preys on small mammals in open country, including grasslands and marshes at all elevations. Partly migratory.

Distribution and variation. Eurasia, New World, reaches oceanic islands. It occurs disjunctly in the Nearctic, Middle America, the West Indies, and South America. It ranges from Surinam W through northern Venezuela, SW through the Andes of Colombia, Ecuador, western Peru, southern Bolivia, all of Chile and Argentina to Tierra del Fuego, and NE to Mato Grosso, São Paulo, and Rio Grande do Sul. This range SE of southern Peru is occupied by *A. f. suinda*, a race larger and darker brown than the more northern *bogatensis*. *Asio flammeus suinda* inhabits the entire chaco in marshy and grassy areas; presumably it is very local in the dry central chaco. The race ranges beyond the chaco in all directions.

FAMILY NYCTIBIIDAE

Nyctibius griseus
Common Potoo

Taxonomy. Polytypic. Sympatric with the other potoos.

Ecology. A large nocturnal forest and woodland bird that captures insects on the wing, and nests on branches, laying one egg. Territorial, nonmigratory.

Distribution and variation. Middle and South America. In the latter, occurs S to Ecuador in the W, and throughout the eastern lowlands to Tucumán, Santa Fe, and northern Uruguay. *Nyctibius griseus cornutus* is a weakly differentiated subspecies, of moderate size and dark overall showing very little white, found from the Amazon and Madeira rivers S throughout southern Brazil, northern and eastern Bolivia, Paraguay, northeastern Uruguay, and Argentina (S to La

Rioja, Chaco, Santa Fe, and Corrientes). The chaco marks the southern extreme of the species' range. It occurs throughout the chaco, except the central Argentine chaco, and it extends beyond to the W (slightly), the N, and the E.

FAMILY CAPRIMULGIDAE

Caprimulgus rufus
Rufous Nightjar

Taxonomy. Comprises a superspecies with Nearctic *C. carolinensis* (Mayr and Short, 1970). Possibly two species are involved in the *rufus* complex, which includes the *minimus* group of southern Middle America to Venezuela (see Meyer de Schauensee, 1966).

Ecology. A forest nightjar, strictly nocturnal in habits, nesting on the ground.

Distribution and variation. New World, Costa Rica and St. Lucia S in lowlands to Tucumán and Santa Fe, Argentina, and Rio Grande do Sul; absent from western South America S of northern Colombia and from all of western Amazonia. *Caprimulgus rufus rutilus*, a rather weakly defined race, occupies the southern portion of the species' range, from eastern Bolivia, central Mato Grosso and Rio de Janeiro S to Tucumán, western Paraguay, northern Santa Fe, Corrientes, and Rio Grande do Sul. This form is rather pale, the markings standing out because some white is evident; little rufous in its plumage. It is found throughout the chaco, except for the xeric central Argentine portion. The chaco forms its southern limit in the SW. It extends W into the dry subtropical forest, E to the Atlantic Ocean, and N to the extent indicated above for this race.

?*Caprimulgus cayennensis*
White-tailed Nightjar

Taxonomy. Polytypic. Relationships not fully established. The southern disjunct form, *candicans*, variously is treated as a species (it would with *cayennensis* comprise a superspecies) or, as here, conspecific with *cayennensis*. It is very similar in all respects to *cayennensis*, differing mainly in the loss of white in the outer primaries of males.

Ecology. Probably nocturnal, aerial foraging, and ground nesting, but very little known.

Distribution. Southern Middle America,

South America. Occurs across the northern part of South America from central Colombia to French Guiana, including Venezuela and immediately adjacent Brazil, and in southern Mato Grosso and adjacent western São Paulo and northeastern Paraguay. It seems likely to occur along the Paraguay River, hence in the Mato Grosso chaco and perhaps in adjacent Santa Cruz, Bolivia, and the Paraguayan chaco.

Caprimulgus parvulus
Little Nightjar

Taxonomy. Polytypic. Its relationships with other nightjars are unclear. *Caprimulgus parvulus anthonyi*, a distinctive, small form from western Ecuador and adjacent Peru may be specifically distinct (Meyer de Schauensee, 1970).

Ecology. Not well known, although common in forests, savannas, desert scrub, and brushland or small woods in the northern pampas. Migratory, in part.

Distribution and variation. Endemic South American. Isolates of restricted distribution occur in northwestern Peru and western Ecuador (*anthonyi*), and in northeastern Colombia and disjunctly in north-central Venezuela (*heterurus*). *Caprimulgus parvulus parvulus* occupies the major part of the species' range, that is, from eastern Bolivia, Mato Grosso, and Maranhão S through all of southern Brazil, Paraguay, and Uruguay, to Tucumán, Córdoba, and Buenos Aires. This form inhabits all of the chaco, and extends beyond it slightly to the W and S, and much farther to the E and N. It occurs as a migrant from western Amazonia (eastern Peru) E to the S of the Amazon River through Pará to the mouth of the Amazon. *Caprimulgus parvulus parvulus* like *heterurus* (which resembles it to a much greater extent than does *anthonyi*) is large, but has somewhat less white in the wings, and less white (more obscured by rufous) in the tail; it also tends to be paler and more rufescent below than *heterurus*.

Hydopsalis brasiliiana
Scissor-tailed Nightjar

Taxonomy. Polytypic. Related to the largely allopatric *H. climacocerca*, but different morpho-

logically, and not forming a superspecies with it.

Ecology. Ground nesting, living in forest edge, woodland, and open country. Migratory in the S.

Distribution and variation. Endemic in South America. A disjunct population is isolated in east-central Peru. Otherwise, occurs from the Amazon River and Purus River S throughout southern Brazil, northern and eastern Bolivia, Paraguay and Uruguay to the northern fringes of Patagonia. The larger, paler, less rufous *H. b. furcifera* occurs S of the nominate form, from eastern Bolivia, central Mato Grosso and São Paulo southward. Its range includes all the chaco and extends beyond in all directions including W into the lower Andean foothills.

Eleothreptus anomalus
Sickle-winged Nightjar

Taxonomy. Monotypic genus, species, relationships uncertain.

Ecology. A peculiar, open country and forest edge species, favoring vicinity of water.

Distribution. Endemic in southeastern Brazil, Uruguay, eastern Paraguay, and Santa Fe, Chaco, and Buenos Aires, Argentina. Known from the chaco only in eastern Chaco and northern Santa Fe, but it probably occurs in eastern Formosa and Corrientes as well.

Podager nacunda
Nacunda Nighthawk

Taxonomy. Polytypic. Monotypic genus, close to *Chordeiles*.

Ecology. Lives on forest edge, campo, savanna, woodland, and pampas; crepuscular and nocturnal in habits; nests on the ground.

Distribution and variation. Endemic in South America, in two disjunct populations. A northern form occupies northeastern Colombia, Venezuela, Guyana, Surinam, and adjacent Brazil. South of the Amazon *P. n. nacunda*, a much larger subspecies with more white in the tail (males), occurs from the Jurua River, Mato Grosso, and Piauí S through eastern Bolivia and Brazil, Paraguay, Uruguay, and northern Argentina to Mendoza, La Pampa, and Buenos Aires.

The race *nacunda* occurs throughout the chaco and beyond it in all directions.

?Chordeiles acutipennis
Lesser Nighthawk

Taxonomy. Polytypic. Related closely to sympatric *C. minor*.

Ecology. Frequents lowland open areas of all types, including savanna, deserts, and forest clearings. Partly migratory. Diurnal to some degree, as well as nocturnal, catching insects in flight.

Distribution and variation. Found from southern Nearctic to Peru, Paraguay, and Rio Grande do Sul. In South America one race occurs in western Ecuador and Peru, and *C. a. acutipennis* is found elsewhere, namely from northern and western Colombia, Venezuela, and the Guianas S through the lowlands to northern Bolivia, the fringe of Paraguay, and Rio Grande do Sul. Of questionable occurrence in the chaco, but possibly reaches the pantanal area of Paraguay and Mato Grosso. *Chordeiles acutipennis acutipennis* is the darkest and most rufous ventrally of the several subspecies of this nighthawk.

Lurocalis semitorquatus
Semicollared Nighthawk

Taxonomy. Polytypic species. Monotypic genus, near *Chordeiles*.

Ecology. Primarily a forest nighthawk; partly migratory. A nocturnal insect forager.

Distribution and variation. New World, Nicaragua discontinuously to northeastern Argentina and Rio Grande do Sul. The distinctive *semitorquatus-rufiventris* group occurs in Middle America, in the Andes of Colombia, northern Venezuela, southern Venezuela, the Guianas and the Rio Negro region of Brazil, and eastern Ecuador and eastern Peru. The southern *L. s. nattereri* is larger than the other lowland races to the N, it is paler, less black marked, and heavily barred below. It occurs S from the Amazon to Mato Grosso, and, probably disjunctly, in southern Brazil from Bahía to Rio Grande do Sul, and inland to eastern Paraguay, eastern Formosa, and Misiones. Possibly specifically distinct, it reaches the fringe of the chaco only in the riparian woods of eastern Formosa.

FAMILY APODIDAE

?Cypseloides rothschildi
Rothschild's Swift

Taxonomy. Monotypic. I consider Nearctic, West Indian, and Middle American *niger*, Colombian *lemosi*, northwestern Argentine (Salta, Santiago del Estero, Tucumán) *rothschildi*, and southeastern Brazilian (Espírito Santo to Rio Grande do Sul) *fumigatus* as species comprising a superspecies. *Cypseloides niger* is large, blackish, with extensive white on the lores and forehead, white on the belly of males and (usually) barred belly of females. Smaller than *niger*, *C. lemosi* is blackish, with less white on the face, no barring below, and a white breast patch. *Cypseloides fumigatus* is brown-black, with little ventral barring and little or no white on the face. Although usually merged in *fumigatus*, *rothschildi* seems specifically distinct (see Meyer de Schauensee, 1966) by virtue of its much paler brown color (grayer anteriorly), its lack of white on the face, its larger size, and its softer tail.

Ecology. Virtually unknown; presumably requires cliffs for nesting purposes.

Distribution. Endemic in South America, range as stated above. May migrate N to Bolivia and Peru. Found in the chaco of western Santiago del Estero, but perhaps foraging E from the Andean foothills where it probably nests, or as a post-breeding wanderer.

Chaetura andrei
Ashy-tailed Swift

Taxonomy. Polytypic. Relationships with congeneric swifts unclear.

Ecology. Forages for insects in small groups over forests or woodlands and adjoining open areas. At least partly migratory, and also may wander after breeding. Apparently a cliff-nesting swift, but perhaps uses hollow trees as well.

Distribution and variation. Endemic in South America in two disjunct populations, one in eastern Venezuela, Guyana, and Surinam, and the other, *C. a. meridionalis*, in southern Brazil (Rio de Janeiro to Rio Grande do Sul; inland N to Piauí, W to Mato Grosso), southeastern Bolivia, most of Paraguay, Misiones, Salta, and Tucumán in Argentina, and perhaps elsewhere in the eastern chaco (Chaco, Santa Fe) and western chaco

(Santiago del Estero) where it is known to occur at least as a post-breeding wanderer. This southern race is distinctly larger and also paler than the northern, nominate form. *Chaetura andrei meridionalis* breeds in most of the chaco, and indeed it may prove to breed throughout the chaco except for the arid central Argentine portion. It extends beyond the chaco to the W (dry subtropical forest) and to the E and NE.

FAMILY TROCHILIDAE

?*Phaethornis pretrei* Planalto Hermit

Taxonomy. Monotypic. Related to *P. augusti* of northeastern Colombia, Venezuela, and Guyana, with which it forms a superspecies. Both have generally similar patterns including a rufous rump, and they are similar in size, bill color, and bill shape. *Phaethornis augusti* differs from *pretrei* mainly in its gray rather than buff underparts, although frequently showing traces of buff.

Ecology. A forest clearing, forest edge, and savanna hummingbird. Nonmigratory.

Distribution. Superspecies endemic in South America. *Phaethornis pretrei* occurs in the Brazilian highlands and campos from Maranhão and Espírito Santo SW to Mato Grosso and (perhaps discontinuously) eastern Bolivia, then S into Salta, Argentina. It reaches the fringe of the chaco in Salta, and possibly in the Santa Cruz chaco. It may occur in western Paraguay, although there are no records for that country.

?*Phaethornis subochraceus* Buff-bellied Hermit

Taxonomy. Monotypic. Relationships within its genus are unclear.

Ecology. Virtually unknown.

Distribution. Endemic in central South America, occupying a very restricted range in Santa Cruz, Bolivia, and adjacent Mato Grosso. It probably occurs in the fringes of the chaco in these areas.

Eupetomena macroura Swallow-tailed Hummingbird

Taxonomy. Polytypic species, monotypic genus.

Ecology. Inhabits forest edges and savannas.

Distribution. Endemic in South America, from the Guianas, the mouth of the Amazon and Amazonia (including southeastern Peru) S of the Amazon River through northern and eastern Bolivia, and central Brazil to São Paulo and the northern edge of Paraguay. The northern Paraguayan chaco and the chaco of Santa Cruz and Mato Grosso are occupied by *E. m. macroura*, a weak race distinguished by its generally bluer color than the other two subspecies. This race occurs in most of the range of the species, except in the far W and the far E.

Colibri serrirostris White-vented Violetear

Taxonomy. Monotypic. Relationships with other congeneric species are unclear.

Ecology. Frequents forest and forest edges. Nonmigratory, but possibly wanders.

Distribution. Endemic in central South America, somewhat discontinuously in northern and eastern Bolivia, in Mato Grosso to Rio de Janeiro (and from Goiás S to Paraná), in Tucumán, and in Santa Fe, Argentina. It occurs in the fringes of the chaco in Santa Cruz, Bolivia, and in Mato Grosso, and also in Tucumán and in the chaco of Santa Fe. It seems unlikely that the Argentine records are indicative of isolated populations; rather, the species may be of sporadic occurrence throughout the chaco, or the southern records may represent post-breeding wanderers.

Anthracothorax nigricollis Black-throated Mango

Taxonomy. Monotypic. Tentatively considered to comprise a superspecies with *A. prevostii*. The latter occurs disjunctly from Mexico to Panama, in northern Venezuela, in southwestern Colombia, and in western Ecuador and adjacent northwestern Peru. Females of these two species are virtually identical (slightly less white in the tails of *nigricollis*), whereas males of *nigricollis* differ from *prevostii* only in lacking green in the blue border of the black throat and breast. Sympatry occurs to a very limited extent in Panama, and in Venezuela, where there may be ecological separation; at any rate the amount of sympatry is very small compared with their allopatric ranges.

Ecology. Little known, but apparently a forest edge and brushland species. Feeds at flowers for nectar and insects, like most hummingbirds, and also takes some insects from the air (Wetmore, 1968). Nonmigratory.

Distribution. Mainly South American, from eastern Panama and northern Colombia E to Venezuela and the Guianas, and S throughout the lowlands E of the Andes to northern and eastern Bolivia, northern Paraguay in the W, all of eastern Paraguay, Corrientes, Argentina, and the northern edge of Uruguay. It occurs in the northern chaco (northern Paraguayan chaco, Santa Cruz, Mato Grosso), and from there to the NW, N, and E.

Chlorostilbon aureoventris
Glittering-bellied Emerald

Taxonomy. Polytypic. Relationships unclear in this difficult genus.

Ecology. A forest, forest edge, and brushland hummingbird that forages in open country as well as in adjacent woodlands.

Distribution and variation. Endemic in South America. Occurs from Maranhão and Pernambuco S to Buenos Aires, and W to northern Bolivia and Mendoza, Argentina. Of the several races, *C. a. aureoventris* occurs virtually throughout the chaco, and N to northern Bolivia and central Mato Grosso, W to the foothills of the Andes Mountains from Bolivia to Mendoza, S to Mendoza, San Juan, and western Santa Fe. Apparently *C. a. lucidus* replaces *aureoventris* in eastern Santa Fe, Corrientes, and eastern Paraguay; it occurs N to Paraná and eastern Paraguay, E to the Atlantic Ocean, and S to central Buenos Aires. From *lucidus*, *aureoventris* differs in having a more golden, less green back, and less blue in the throat.

?*Thalurania furcata*
Fork-tailed Woodnymph

Taxonomy. Strongly polytypic. Sympatric with its near relatives.

Ecology. Inhabits forests, foraging on insects and nectar at various flowers (including Heliconia; Wetmore, 1968). Nonmigratory.

Distribution and variation. Middle and South America, in W to Ecuador, and in E throughout the lowlands to southern Bolivia, Tucumán, east-

ern Paraguay, and São Paulo. The southern *furcata* group may be specifically distinct from the glittering-crowned *colombica* group, occurring S and E to western Venezuela (Meyer de Schauensee, 1966; Wetmore, 1968). Variation in color, and extent of tail forking is extreme in this species. The rather weakly defined race (tail relatively short, blue-violet reduced on upper back of male) *baeri* occurs from southern Bolivia, and probably Tucumán, through eastern Bolivia, Mato Grosso, Goiás, and to Maranhão and Bahia in the E. This form probably occurs in the chaco portions of Santa Cruz and Mato Grosso and perhaps in northernmost Paraguay.

Hylocharis sapphirina
Rufous-throated Sapphire

Taxonomy. Monotypic. Relationships unclear in *Hylocharis*.

Ecology. Not well known, occurs mainly in forests.

Distribution. Endemic in South America, disjunct in the north from the Guianas W to Venezuela, eastern Colombia, eastern Ecuador, and eastern Peru, and then E along the Amazon River and S of it to its mouth (hiatus N of Amazon in the E), and in southern Brazil (Bahía to Rio de Janeiro and São Paulo) to eastern Bolivia, central Paraguay, and Formosa, Chaco and Misiones, Argentina. Thus the two populations are separated by the campo region and southern Amazonia. The eastern chaco from the eastern Paraguayan chaco S through eastern Formosa to eastern Chaco forms the western border of the species' range in the south. Its reported occurrence in Entre Ríos needs verification.

Hylocharis chrysura
Gilded Hummingbird

Taxonomy. Monotypic (see Naumburg, 1930). It is uncertain to which of the other congeneric species it is most closely related.

Ecology. Occupies forest edge and savanna; wanders about brushy areas in open country as well as in woodlands. Usually the commonest chaco hummingbird.

Distribution. Endemic in south-central South America, from northern Bolivia E to Minas Gerais, and S to Tucumán, Buenos Aires, and Uruguay. It occurs throughout the chaco, and

beyond it slightly to the W, to the N (central Mato Grosso), E, and SE, but not directly to the S (found in riparian brushland and woodland along the Parana River S of Santa Fe).

Polytmus guainumbi
White-tailed Goldenthrout

Taxonomy. Polytypic. Not very closely related to its nearest relatives in *Polytmus*.

Ecology. Little known. Occurs in savannas and forest edges.

Distribution and variation. Endemic in South America. Two contiguous races comprise the northern range (eastern Colombia E through southern Venezuela and northern Brazil to the Guianas and Amapá), disjunct from that of southern *P. g. thaumantias*. The latter is larger than the northern forms, and it has less white in the tail. Its range includes eastern Bolivia, the eastern Paraguayan chaco, eastern Formosa, and Corrientes, NE through eastern Paraguay and Mato Grosso to Goiás and Maranhão. Within the chaco it is restricted to the pantanal and eastern edge of the more moist eastern chaco woodland.

Amazilia chionogaster
White-bellied Hummingbird

Taxonomy. Polytypic. Closely related to sympatric *A. viridicauda*.

Ecology. A forest species, also found at woodland edges.

Distribution and variation. Endemic in South America, chiefly subtropical dry forest and scrub bordering the eastern Andes from northern Peru to Tucumán, Argentina, but also found perhaps disjunctly in western Mato Grosso and in eastern Formosa. Occurs in the chaco in eastern Formosa, where its status (possibly wandering birds or migrants) is unclear, but may occur sporadically across the northern chaco. The southern race (from northern Bolivia E and S) *hypoleucus* is smaller and paler green above than the nominate race.

Heliomaster furcifer
Blue-tufted Starthroat

Taxonomy. Monotypic. Related to the essentially allopatric *H. squamosus*, but not very closely.

Ecology. Common along forest edges and in woodlands, savannas, and brushy or riparian areas in pampas.

Distribution. Endemic in South America. A disjunct population apparently occurs in southeastern Colombia (Meyer de Schauensee, 1966); otherwise from central Bolivia E to Goiás, and S through eastern Bolivia, Mato Grosso, and Paraguay to Uruguay and southern Rio Grande do Sul in the E and to Catamarca, Córdoba, and northern Buenos Aires in the W. Thus, it occurs throughout the chaco and beyond it in all directions, although only slightly to the W and S.

FAMILY TROGONIDAE

Trogon rufus
Black-throated Trogon

Taxonomy. Polytypic. No very close relative in *Trogon*.

Ecology. A forest trogon of lowland areas. Feeds on insects and fruits, and nests in holes in trees.

Distribution and variation. New World, Middle America to central South America. Occurs in South America from western Ecuador N to northern Colombia, then E to the Guianas and S through Amazonia, but not the lower Amazon region, to Mato Grosso, central and eastern Paraguay, Misiones, Paraná, and NE to Bahía. Of the three races, the southern *chrysochloros* is largest and males are bluer anteriorly. This race occurs from northern Mato Grosso, the eastern Paraguayan chaco (*fide* Olog), eastern Paraguay and Misiones E and NE to Bahía. Thus it is found in the northeastern chaco of eastern Paraguay and adjacent Mato Grosso.

Trogon surrucura
Surucú Trogon

Taxonomy. Polytypic. The eastern race *aurantius* is very distinct and has been treated as a species. Females are white-bellied, rather than pink-bellied as in western nominate *surrucura*, and males are more purple anteriorly, bluer and less green above, with more white in the tail, and washed out yellowish-pink, rather than pink, below.

Ecology. Found in forests, forest edges, and

woodlands, including gallery forests in savanna country.

Distribution and variation. Endemic in east-central South America from the eastern chaco through Misiones, eastern Paraguay and Mato Grosso to southern Bahía and the Atlantic Coast S to Rio Grande do Sul. The distinctive western race (see above) *surrucura* occurs in the eastern chaco (eastern chaco woodland and pantanal from southern Mato Grosso and the eastern Paraguayan chaco S through eastern Formosa, and eastern Chaco to northern Santa Fe) and eastward to São Paulo and Minas Gerais.

Trogon curucui

Blue-crowned Trogon

Taxonomy. Polytypic. Relationships unclear within *Trogon*.

Ecology. Found in forest, woodland, and savanna. Nonmigratory, as are all trogons.

Distribution and variation. Endemic in South America. Found in lowlands from southeastern Colombia, eastern Ecuador, eastern Peru, western Amazonian Brazil, central Pará, and Maranhão S through central and southern Brazil, and northern and eastern Bolivia to Salta, Argentina, western and northeastern Paraguay, and Rio Grande do Sul. A weak race, *behni*, occurs in the northern chaco (northern Paraguayan chaco, Santa Cruz, Mato Grosso), and from there W to the dry subtropical forest along the Andes, NW to central Bolivia, N to north-central Mato Grosso, and E to eastern Mato Grosso. *Trogon curucui behni* is somewhat more bronze-backed than are the other two subspecies.

FAMILY ALCEDINIDAE

Ceryle torquata

Ringed Kingfisher

Taxonomy. Polytypic. Forms a superspecies with Nearctic *C. alcyon*. These species have their closest relatives in the tropical Old World (*C. maxina*, *C. lugubris*), and they most likely reached the New World from Africa, becoming less barred and bluer in the course of their evolution. *Ceryle torquata* is larger than *alcyon*, is more barred under the wings and around the vent, and has a rusty abdomen (*alcyon* is white

bellied, but females occasionally have rufous on the belly).

Ecology. Much as *alcyon*, solitary, or pairs scattered along larger streams and rivers, as well as lakes, swamps and marshes. Migratory in S. *Ceryle torquata* reaches the cool-temperate southern tip of South America, but is tropical in northern Middle America where its range approaches that of *alcyon*. Nests in holes in banks.

Distribution and variation. New World, Mexico to Tierra del Fuego. The race *torquata* occurs from Mexico to central Chile and Buenos Aires, where it is replaced by a similarly sized but more chestnut-bellied form. *Ceryle torquata torquata* inhabits the entire chaco although it is local because it needs large bodies of water. It may be absent from the central chaco, particularly in Argentina. It extends beyond the chaco in all directions.

Chloroceryle amazona

Amazon Kingfisher

Taxonomy. Polytypic. Related to other sympatric species, e.g., smaller *C. americana*.

Ecology. Water-dependent and fish-foraging, found along streams of all sizes, lakes, and sea-coast. Usually in forested or partly wooded areas, but penetrating the northern pampas.

Distribution. Middle and South America, represented in the latter by the small *C. a. amazona*, occurring from northern Colombia E and S (status along western coast of Ecuador uncertain) through the lowlands as far as La Rioja and Buenos Aires, Argentina. This form occurs throughout the chaco, slightly beyond it to the W (foothills of Andes) and the S (to Córdoba, northern Buenos Aires), and far to the N and E.

Chloroceryle americana

Green Kingfisher

Taxonomy. Polytypic. Probably related closely to *C. amazona*.

Ecology. As *C. amazona*, but occurring as well along smaller streams, and in swampy woodlands, and wooded or brushy streams in drier areas than *amazona*. Nonmigratory.

Distribution and variation. Southern edge of North America, Middle America, and South

America. Occurs S in South America to northern Chile W of the Andes, and throughout the eastern lowlands from northern Colombia and the Guianas to Mendoza and northern Buenos Aires, Argentina. *Chloroceryle americana mathewsi* is a large race with a proportionally finer bill, found in the southern part of the species' range from eastern Bolivia, northern Mato Grosso, and Bahía S through southern Brazil, Paraguay, and Uruguay to northern Buenos Aires, Córdoba, and Mendoza, Argentina. It is found throughout the chaco, and beyond it in all directions.

FAMILY MOMOTIDAE

Momotus momota Blue-crowned Motmot

Taxonomy. Polytypic. Related species sympatric.

Ecology. Nests in tree holes in forests, forest clearings, savannas, and cultivated (wooded) areas. Forages by darting from perch after insects and fruits.

Distribution and variation. Middle America and South America, S in the W to northwestern Peru, and in the E through the lowlands to the eastern corner of Brazil, Goiás, western São Paulo, northern Paraguay, and Salta, Argentina. Among the many weakly to strongly differentiated subspecies (possibly more than one species is involved), *Momotus momota pilcomayensis* is barely separable from Bolivian *nattereri* by virtue of its less blue-violet wings and perhaps slightly larger bill. Both are purple-naped, show little rufous below, and have a full racket tail. The race *pilcomayensis* occurs from Salta and Jujuy to central Bolivia and E across eastern Bolivia and the northern Paraguayan chaco to Mato Grosso, western São Paulo, and the northern edge of eastern Paraguay. It is found in the northern chaco (Bolivia, Mato Grosso, northern Paraguay).

FAMILY BUCCONIDAE

?*Notharchus macrorynchus* White-necked Puffbird

Taxonomy. Polytypic. Relationships are not well established in *Notharchus*.

Ecology. Inhabits forest, nests in a hole in the ground. Insectivorous. Nonmigratory.

Distribution and variation. Middle and South America. Somewhat discontinuously distributed in western Ecuador and adjacent Peru, in central Colombia, from northern Colombia E to the Guianas and Maranhão, W to eastern Peru and eastern Ecuador, S through Amazonia to northern and eastern Bolivia and at least northern Mato Grosso, and from eastern Paraguay and Misiones E through Santa Catarina and NE along the coast to Espírito Santo. The distinct southeastern race *swainsoni*, sometimes considered a separate species, has rufous rather than the white underparts of the northern forms, and it has less white on the forehead. This race appears not to contact northern populations; there apparently is a hiatus in Mato Grosso. *Notharchus macrorynchus swainsoni* possibly occurs in the chaco, as it reaches the eastern bank of the Paraguay River. Specimens ascribed to "Riacho Negro," far out in the Paraguayan chaco, are probably from eastern Paraguay (Short, 1972a).

Nystalus maculatus Spot-backed Puffbird Figure 32

Taxonomy. Polytypic. Related rather closely to the largely allopatric *N. striolatus*.

Ecology. Largely a woodland and woodland edge species found in the caatinga, campo, and chaco regions. Perches low in bushes and trees, darting out to foliage or the ground after its prey, chiefly insects. Nonmigratory.

Distribution and variation. Endemic in South America. From eastern (central?) Bolivia and the subtropical forest bordering the Andes of Argentina S to La Rioja E through the chaco and Mato Grosso to Pará, Maranhão, Ceará, and Bahía. *Nystalus maculatus striatipectus* is barely distinct from adjacent (Bolivia, Mato Grosso) *pallidigula*, chiefly by virtue of its larger size; these two races, inhabiting the area SW of central Mato Grosso, are streaked below rather than spotted, as are the two subspecies from northeastern Brazil. All the chaco is inhabited by *striatipectus*, which extends beyond the chaco only slightly (SW to La Rioja and Córdoba, W to the dry subtropical forest, N to central Bolivia; its eastern border is the Paraguay-Parana river, and the pantanal of Mato Grosso).

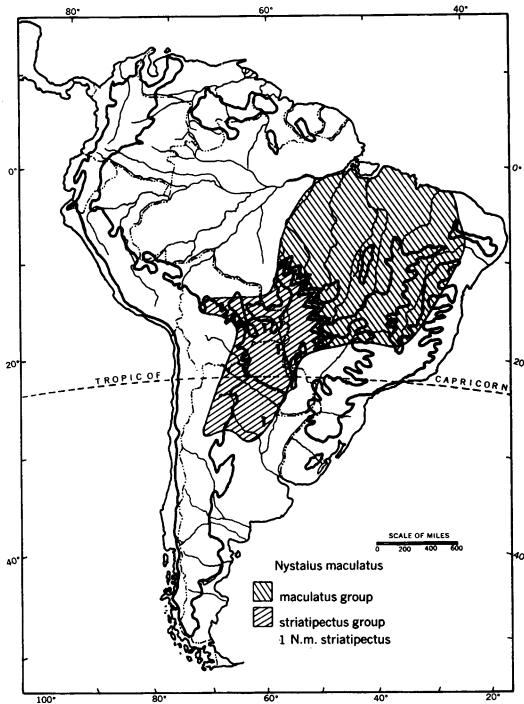


FIG. 32. Range of Spot-backed Puffbird (*Nystalus maculatus*). A campo-caatinga-chaco-dry subtropical forest species, with intergrading subspecies groups, as shown. The race *striatipectus* is restricted to chaco and subtropical dry forest.

FAMILY RAMPHASTIDAE

?*Pteroglossus castanotis* Chestnut-eared Araçari

Taxonomy. Polytypic. Forms a superspecies with *P. aracari* of eastern Venezuela and the Guianas and eastern Brazil coastally S to Santa Catarina and inland only to Pará and Minas Gerais. Both species have a similarly shaped bill, lack a black breast band or mark, and show less red in the plumage than do other araçaris; *aracari* and one race of *castanotis* also have green in the thighs. They differ in the blacker, more restricted yellow bill pattern of *castanotis*, the reduction of brown in *aracari* to traces in the ear coverts and brown in the throat of some races (versus brown in the ear coverts, upper back, throat, and occasionally the thighs of *castanotis*) and the redder abdomen of *castanotis*.

Ecology. Mainly fruit-eating; inhabits forests

and savannas; nests in holes in trees. Nonmigratory.

Distribution and variation. Superspecies endemic in South America. *Pteroglossus castanotis* occurs from southeastern Colombia, eastern Ecuador, eastern Peru, and western Amazonia SE through lowland Bolivia and Mato Grosso to eastern Paraguay, Misiones, and western São Paulo. The southeastern of the two races, *australis*, occurring from eastern Bolivia and Mato Grosso S, is less chestnut and more rufous, brown rather than black in the crown, and its thighs are fully rufous rather than mixed with green as in the nominate race. *Pteroglossus castanotis australis* occurs on the northeastern fringes of the chaco in Santa Cruz, Bolivia, and in southern Mato Grosso, as well as along the Paraguay River S to Asunción (undoubtedly it forages along the western side of the river).

Ramphastos dicolorus Red-breasted Toucan

Taxonomy. Monotypic. I am not certain to which of the other toucans of its genus it is most closely related.

Ecology. Large, frequents forest, but ranges into the pantanal. Nests in holes. Feeds on all manner of fruits, insects, and probably occasionally small vertebrates.

Distribution. Endemic in central South America, from Goiás and São Paulo to central Paraguay, Corrientes, and Rio Grande do Sul. Found in the east-central chaco within the pantanal and eastern edge of the eastern chaco woodland, from northern Paraguay S to eastern Chaco Province; extends E and NE from there, the eastern chaco forming the western border of the species' range.

Ramphastos toco Toco Toucan

Taxonomy. Polytypic. Not very closely related to others of its genus.

Ecology. Very large, far-ranging, found in forests, savannas, and cultivated areas. Nests in holes in trees, moves about in small bands. Feeds on fruits, probably also small animals.

Distribution and variation. Endemic in South America, from the Guianas, eastern Amazonia and

northeastern Brazil generally, S and SW to Minas Gerais (not in coastal eastern Brazil SE of Piauí), western Rio Grande do Sul, eastern Paraguay, northern Santa Fe, Mato Grosso, and Salta, Argentina. Two races are generally recognized, a southeastern (S and E from Goiás and Mato Grosso) form *albigularis*, and *toco*, supposedly occurring in the eastern Amazon region and SW to Jujuy and Salta, Argentina. I find that birds from northwestern Argentina and most of eastern Bolivia cannot be assigned to either race. The race *albigularis* is white-throated, whereas *toco* has yellow and red at the rear of the throat, and faint yellow (possibly due to fading in older specimens) throughout the otherwise whitish throat. The northwestern Argentine and south-central Bolivian birds are faintly yellowish to white-throated (not richly yellow as is *toco*, and lacking orange-red); furthermore, in contrast with *toco* and *albigularis*, adults have a very narrow black base of the bill. These may represent an undescribed race. Within the chaco, *albigularis* occurs in the pantanal from Mato Grosso S to northern Santa Fe (hence eastern edge of chaco) and E from there. *Ramphastos toco toco* occurs in northernmost western Paraguay, adjacent Santa Cruz, Bolivia, and the northern pantanal of Mato Grosso. In far western Paraguay and Salta, adjacent to the chaco, and to the W, occurs the peculiarly marked southwestern population. Thus, only the central, dry chaco and the southwestern chaco are unoccupied by the species, although its breeding elsewhere in the chaco may be extremely local.

FAMILY PICIDAE

Picumnus cirratus White-barred Piculet

Figure 33

Taxonomy. Polytypic. Forms a superspecies with subtropical forest (along Andes in Peru, and Bolivia to Jujuy and Salta, Argentina) *P. dorbygnianus*. The latter is scaly-breasted whereas *cirratus* is barred. The situation is complicated by several factors. *Picumnus cirratus thamnophiloides*, considered by some a separate species, occurs sympatrically with *P. dorbygnianus* in Salta and southern Bolivia; it is partly barred, scalloped, with very white below, that is somewhat

intermediate between *cirratus* and *dorbygnianus*. Furthermore, *dorbygnianus* strongly tends toward central Brazilian *albosquamatus-guttifer* of the *P. minutissimus* complex, which generally replaces *dorbygnianus-cirratus*, although some sympatry (of *dorbygnianus-albosquamatus*, *cirratus-guttifer*) appears likely. In addition the northern disjunct form of *P. cirratus*, namely the *macconnelli* group (two races in the Guianas to lower Amazon, broadly sympatric with *minutissimus*), is markedly different from both southern *cirratus* and *dorbygnianus* in its heavy bill, stronger ventral barring, and lack of dorsal markings, making the situation more complex. Personally, appreciating the rather small number of species of piculets that coexist at any one locality (usually no more than two or three species

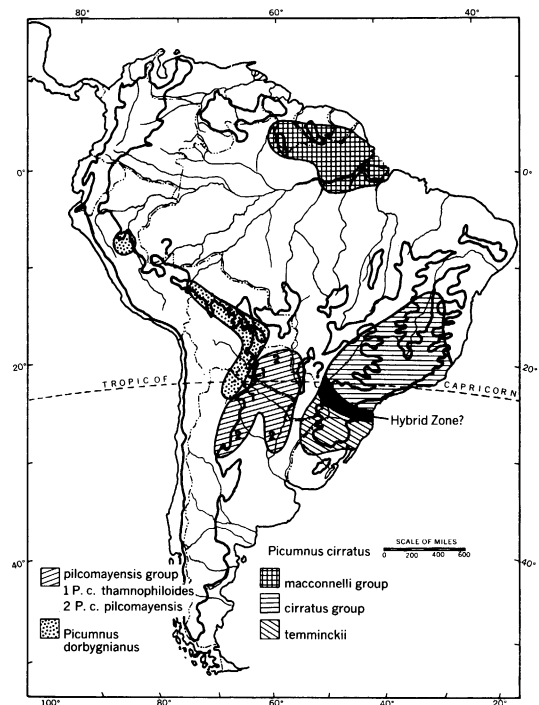


FIG. 33. Range of superspecies *Picumnus cirratus*. Shown stippled are disjunct races of Andean *P. dorbygnianus*, and by various lines, White-barred Piculet, *P. cirratus*. There are four distinct groups of *P. cirratus*; two are disjunct, as shown, and other two apparently hybridize as indicated. *Picumnus cirratus pilcomayensis* inhabits chaco and dry subtropical forest (see text).

occur together) and the usually very strong differences among sympatric species, I find it difficult to accept the specific status of *dorbygnianus* and *cirratu*s, let alone *thamnophiloides*. The *macconnelli* group on the contrary appears more strongly differentiated than are *dorbygnianus*, southern *cirratu*s, and *albosquamatus*. Possible explanations for this apparent dilemma might include the hybridization of *cirratu*s and *dorbygnianus* to produce *thamnophiloides*, for example. Tentatively I maintain *dorbygnianus* and *cirratu*s as species comprising a superspecies, although clearly the situation requires study. Another element of this superspecies may be *P. temminckii*, of eastern Paraguay and Paraná to Rio Grande do Sul, which is merged into *cirratu*s

by K. Stager (in prep.); it interbreeds with *cirratu*s in northern Paraná and São Paulo.

Ecology. Southern *P. cirratu*s inhabits forest, woodland, and edge. It works over vines, small trees, branchlets, and bamboo in the manner of a tiny woodpecker, nests in holes excavated in stubs, is territorial, and nonmigratory (see Short, 1970).

Distribution. Endemic in South America, as are all its close relatives. *Picumnus cirratu*s is found in the southern Guianas S to the lower Amazon region (*macconnelli* group, see above), and in southeastern Brazil from Minas Gerais and Espírito Santo SW to southeastern Mato Grosso and Paraná, and after an apparent gap, from southwestern Mato Grosso, central Paraguay (Paraguay River), Corrientes, and western Entre Ríos W through the chaco to southern Bolivia and La Rioja (*cirratu*s group, including *thamnophiloides*). All the chaco except the Bolivian portion is occupied by this species, mainly by the gray-backed, ventrally barred *pilcomayensis* (its range is entirely in the chaco except for a SW extension to La Rioja), of which *tucumanus* is considered a synonym. The scalloped-bellied *thamnophiloides* occurs in the central western fringes of the chaco (southern Bolivia, probably adjacent southwestern Paraguay, and Salta), which is precisely where *P. cirratu*s meets *P. dorbygnianus*.

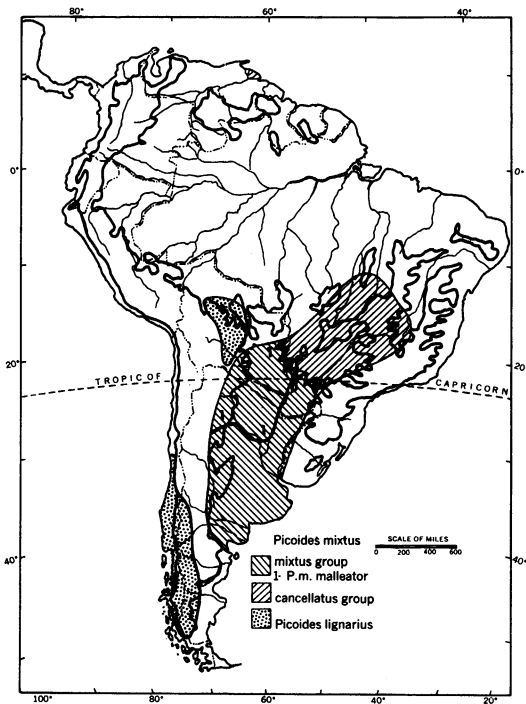


FIG. 34. Range of Checkered Woodpecker (*Picoides mixtus*) and its allospecies *P. lignarius*. Latter has disjunct Bolivian and Fuegian populations. *Picoides mixtus* has racial groups in campo region, and in chaco-chaco scrub-pampas and dry subtropical forest; these apparently interbreed where indicated. *Picoides mixtus malleator* occurs mainly in chaco.

Picoides mixtus
Checkered Woodpecker
Figure 34

Taxonomy Polytypic. Very closely related to, if not conspecific with *P. lignarius* of the Fuegian forests and upland Bolivian dry woodlands. These form a superspecies, related to North and Middle American species of the *scalaris* group (Short, 1971a). *Picoides lignarius* resembles *P. mixtus* closely, differing in its more barred and less scalloped dorsum, and generally in the separation of the red nuchal patch of males into two lateral nuchal spots. The two putative species do not now meet in river valleys northeast of Patagonia (Short, 1970), although they may once have been in contact there. Adjacent populations show no effects of former introgression. A more

likely area of contact is in the lower valleys of the southern Bolivian Andes (Tarija), where dry woodland, lowland *mixtus* seems likely to contact *lignarius*, at least sporadically, although there may be ecological separation of the two; the situation is in need of field study. For the merger of *Dendrocopos* into *Picoides* see Mayr and Short (1970) and Short (1971a).

Ecology. A small brushland and dry woodland species inhabiting the chaco, savannas, campo, and brushy areas in pampas and the northern edge of Patagonia. Primarily a prober and gleaner for insects on or near the surface of bark of twigs and small branches of bushes and trees. Southern populations may undergo slight northward movement in the fall.

Distribution and variation. Superspecies endemic in southern South America. *Picoides mixtus* inhabits the southern campo region of Goiás and Mato Grosso, S to Minas Gerais and São Paulo and SW through the chaco and pampas-forest ecotone of eastern Paraguay, southernmost Bolivia, and all of lowland Argentina S to northern Río Negro; also western Uruguay and probably western Rio Grande do Sul. The entire chaco, with the exception of the Bolivian portion is occupied by this species, represented by the subspecies *malleator*, which is almost confined to the chaco. It extends beyond the chaco only into dry subtropical forest W of the chaco from Tarija, Bolivia S through Tucumán to La Rioja, being replaced by other races to the S, E, and NE of the chaco. *Picoides mixtus malleator* is similar to the other two southern races, *mixtus* and *berlepschi*, from which it differs chiefly by its smaller size. These three forms differ markedly from the much smaller, small-billed, browner, more barred dorsally, and streaked ventrally, *P. m. cancellatus* of Mato Grosso and NE to Goiás and Minas Gerais. This form seems to have evolved in isolation, and it appears to be in secondary contact with *malleator* in southwestern Mato Grosso and with *mixtus* in southern Mato Grosso-northeastern Paraguay. The species as a whole shows clinal diminishment in size from southern *berlepschi* through *malleator* and *mixtus*, to northernmost *cancellatus*, with a definite "step" in the cline where other races meet *cancellatus*.

Melanerpes candidus
White Woodpecker
Figure 35

Taxonomy. Monotypic. A peculiar species, but behaviorally and morphologically not separable generically from *Melanerpes* (see Short, 1970 for merger of "*Leuconerpes*" into *Melanerpes*).

Ecology. Highly social, frequents open woodlands, savannas, and forest edges. It moves long distances across open country to favored foraging sites for fruits and honey, although it also feeds on insects. Nonmigratory.

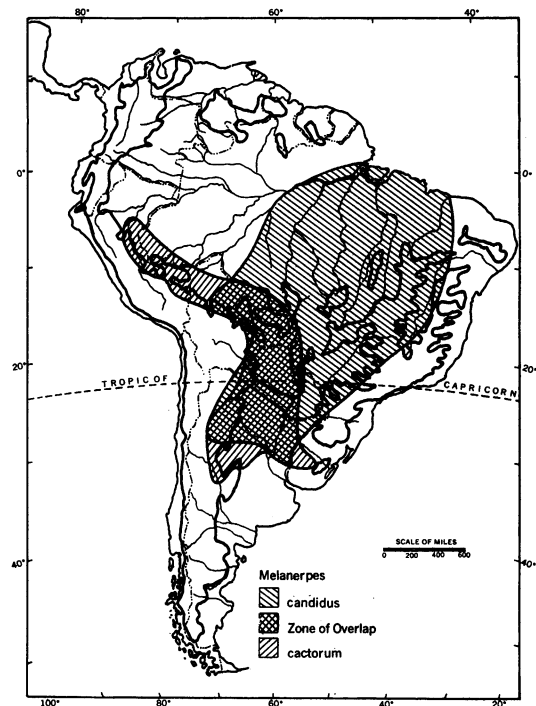


FIG. 35. Range of White Woodpecker (*Melanerpes candidus*) and White-fronted Woodpecker (*M. cactorum*). Former is widespread in semi-open country (campo, Amazonian fringe, chaco, northern pampas, dry subtropical forest), latter occurs in seasonally dry forest and scrub (chaco, subtropical dry forest, drier forests of southeastern Peru). It is not implied that these species are related very closely, and replace one another.

Distribution. Endemic in South America from the lower Amazon River and Maranhão S through interior Brazil, northern and eastern Bolivia, Paraguay, and northern Argentina to La Rioja, Santa Fe, and Entre Ríos. This species inhabits the entire chaco, favoring the pantanal and cultivated areas, but is found at least sporadically everywhere. It extends beyond the chaco slightly to the W into dry subtropical forest, and much farther to the N, NE, and E (to eastern Corrientes, Misiones, São Paulo).

Melanerpes cactorum

White-fronted Woodpecker

Figure 35

Taxonomy. Monotypic. Has no very close relatives, but is typically melanerpine in habits, hence was merged ("*Trichopicus*") in *Melanerpes* by Short (1970). Polymorphic (yellow versus white throat).

Ecology. Common, small, insect- and fruit-eating, semi-social. Inhabits forest edges and woodlands, especially in dry forests. Nests in holes in palms, other trees, and cactus. Nonmigratory.

Distribution. Endemic in South America E of the Andes, but close to them from central Peru to northern Bolivia, then in lower Andean slopes and in the lowlands from eastern Bolivia and southwestern Mato Grosso S through western Paraguay to La Rioja, San Juan, Santa Fe, and Entre Ríos, Argentina, and into western Uruguay. In the E extends away from the Paraguay-Parana rivers only in Corrientes, Entre Ríos, and western Uruguay. It occurs throughout the chaco, and barely beyond it to the W, E, and SE, but extends farther SW (to San Juan), and NW (to Peru).

Veniliornis passerinus

Little Woodpecker

Taxonomy. Polytypic. Forms a superspecies with *V. frontalis* of south-central Bolivia S in dry subtropical forest to Tucumán. Both have reduced red in the plumage and restricted dorsal barring. *Veniliornis frontalis* is larger, more olive and less yellow, with a more spotted crown and (males) forehead, and grayer and blacker ventral bars than *passerinus*.

Ecology. Found in forest, woodland, and brushland in denser arboreal vegetation and more open plant formations, such as savannas and campos. Solitary or in pairs or family groups, territorial, nonmigratory.

Distribution and variation. Superspecies endemic in South America. *Veniliornis passerinus* is found from northern Venezuela SW to eastern Colombia, then E through Amazonia and Pará to Amapá and southern parts of the Guianas, and S through eastern Ecuador, eastern Peru, all of central Brazil, and northern Bolivia to eastern Bolivia, central and eastern Paraguay, northern Santa Fe, central São Paulo, and Bahía. The southern *olivinus*, a very large race with a long bill and dark underparts (narrower white bars than other races), occurs throughout the pantanal area of the chaco, chiefly in riparian woods with bamboo, and beyond this region of the chaco E to eastern Paraguay, and Minas Gerais, NE to north-central Mato Grosso, and N to eastern Santa Cruz.

Piculus chrysochloros

Golden-green Woodpecker

Taxonomy. Polytypic. Forms a superspecies with *P. aurulentus* of Rio de Janeiro to São Paulo, easternmost Paraguay, Corrientes, and Rio Grande do Sul. These species resemble each other in their ventral barring (no tendency toward spotting or streaking), the color pattern of the head generally, and in bill structure and size. *Piculus aurulentus* has barring under the wings, is greener and blacker below, and has two pale facial stripes, whereas *chrysochloros* is unbarred under the wings, yellower green below, and has only a single pale facial stripe.

Ecology. Occurs in woodland and forest, also found in patchy woods in savannas. Feeds on ants. Nonmigratory.

Distribution and variation. Essentially the superspecies is endemic in South America. *Piculus chrysochloros* occurs from eastern Panama, northern Colombia, and western Venezuela S through eastern Colombia and E along the Brazil-Guianan border, and through upper Amazonia (including eastern Ecuador, eastern Peru, northern Bolivia), Brazil, to the S of the lower Amazon River and E to Maranhão, and S through

the interior to Minas Gerais, central Mato Grosso, western Paraguay, and the chaco of Argentina. An apparently isolated population occurs in Rio de Janeiro, where it may meet *P. aurulentus*; otherwise these species seem not to meet. *Piculus chrysochloros chrysochloros* is much smaller in size than northern races (some of which are very well marked); it occurs from Goiás, Bahía, and central Mato Grosso W through the chaco, and not beyond it. Thus, it occurs throughout the chaco except for the Bolivian chaco, the northwestern Paraguayan border, and the small area of chaco east of the Parana River in Corrientes and Entre Ríos.

Colaptes melanochloros
Green-barred Flicker

Taxonomy. Strongly polytypic. Forms a superspecies with the smaller, northern *C. punctigula*, which also has reddish on the breast and scalloped markings on the throat. The latter occurs from eastern Panama and northern Colombia E to Venezuela, through southwestern Venezuela to eastern Colombia, and from there E to Surinam and French Guiana (lacking in Guyana, and southeastern Venezuela) and the area north of the Amazon at its mouth, and S through eastern Ecuador, eastern Peru, northern Bolivia, and Amazonian Brazil to northern Mato Grosso. It apparently fails to meet *melanochloros* (*C. m. nattereri*) in Bolivia and Mato Grosso. Merged in *Colaptes* by Short (1972a).

Ecology. Partly arboreal, partly terrestrial, forages for ants, nests in trees; territorial and essentially nonmigratory. It occupies forests, savannas, brushy areas, and woodlands of the pampas, and desert scrub in Andean valleys.

Distribution and variation. Superspecies endemic in South America, except for *punctigula* in eastern Panama. *Colaptes melanochloros* occurs from Marajo Island and coastal Maranhão throughout eastern and southern Brazil, W to Mato Grosso, and the highland valleys of central Bolivia, through Paraguay, and S along the lower Andean slopes and foothills to Neuquén and Río Negro, as well as Buenos Aires and Uruguay. Two racial groups hybridize where they meet, at least from southern Paraguay to Rio Grande do Sul. These are the greener, generally longer-tailed, plain-breasted *melanochloros* group of northeast-

ern Brazil to eastern Bolivia, Mato Grosso, eastern Paraguay, and northern Rio Grande do Sul, and the semi-terrestrial, browner, shorter-tailed, golden-breasted *melanolaimus* group of highland valleys in Andean Bolivia, the Paraguayan chaco, adjacent southern Bolivia, Argentina from Jujuy to Neuquén and E to Río Negro, Buenos Aires, Uruguay, southwestern Rio Grande do Sul, and western and southern Corrientes (Short, 1972a). Inhabiting the chaco is the weakly differentiated *C. m. nigroviridis* of the *melanolaimus* group, with a range almost coinciding with the chaco, and *C. m. nattereri* of the chaco of Bolivia and probably the pantanal of Mato Grosso. *Colaptes melanochloros leucofrenatus* occupies the southern fringes of the chaco about Tucumán and Santiago del Estero. Belonging to the *melanolaimus* group, it is slightly larger, whiter and less yellow-green than *nigroviridis*. The smallest race, *C. m. nattereri*, is very short-billed, greener and without gold on the breast.

Colaptes campestris
Campo Flicker
Figure 36

Taxonomy. Polytypic. No very close relatives in *Colaptes*.

Ecology. Essentially terrestrial, social, ant-feeding, found in open and semi-open country including savannas, forest edges, and clearings. Nests in trees, termite nests, and banks. Nonmigratory.

Distribution and variation. Endemic in South America. Disjunct populations occur in Surinam, in the lower Amazon Valley, and in east-central South America from Maranhão and Pernambuco S essentially throughout southern Brazil and W to northern Bolivia and central Paraguay and then S through lowland Argentina to San Juan and to Río Negro; in the E to Buenos Aires, Uruguay, and southern Buenos Aires, with an apparent gap between northern Santa Catarina and central Rio Grande do Sul. I recognize (Short, 1972a) two races, sometimes considered species. These are northern *campestris*, from central Paraguay and Santa Catarina northward, and *campes-troides* from southern Paraguay, Misiones, and Rio Grande do Sul southward. These differ mainly in the presence or absence of a black throat patch (present in *campestris*, absent in

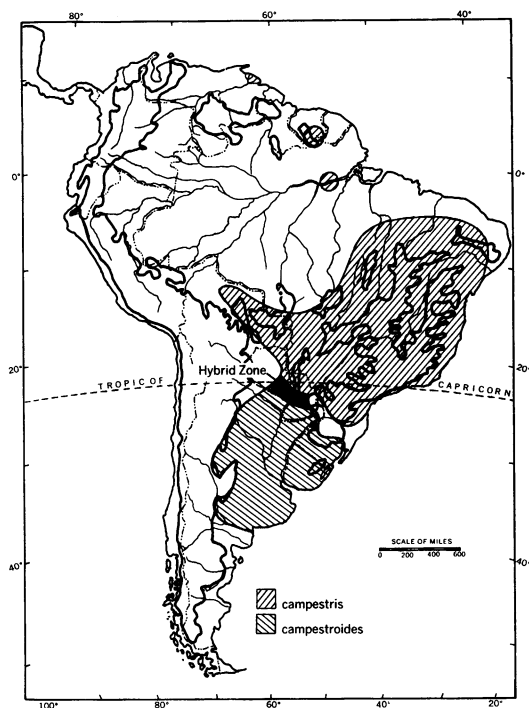


FIG. 36. Range of Campo Flicker (*Colaptes campestris*). Two races of this terrestrial woodpecker, one of campo-caatinga and surrounding open forest areas, and other of pampas and open chaco and chaco scrub, hybridize in Paraguay. Isolates of northern form occur in savanna pockets as shown, suggesting former savanna corridor to the south.

campestroides); all other differences are trivial and involve great overlap. Hybridization occurs in south-central Paraguay, and possibly in Misiones, and appears to involve fully hybrid populations. The contact is secondary, and apparently is being enhanced by clearing of forests. The northeastern chaco is occupied by *campestris* (in Bolivia, southwestern Mato Grosso, northeastern Paraguayan chaco), and, S of the hybrid zone, the southeastern chaco from Formosa and Salta, to the southern extreme and beyond is occupied by *campestroides*. The species seems to be absent from the western chaco of Paraguay and adjacent Argentina, apparently because the dense, arid woodland is unsuitable for them. Within the chaco they are most common in the pantanal.

Celeus lugubris
Pale-crested Woodpecker

Taxonomy. Polytypic. Forms a superspecies with *C. flavescens* (eastern edge of Paraguay, and Misiones through eastern Brazil including Goiás to the mouth of the Amazon, and the lower part of that river valley), *C. elegans* (including the *jumana* group, of Amazonia, eastern Venezuela and the Guianas to the mouth of the Amazon, northern Mato Grosso, and northern Bolivia), and Middle American *C. castaneus*. *Celeus lugubris* meets and hybridizes sporadically with *C. elegans jumana*, and *C. flavescens* overlaps narrowly with *C. elegans jumana*, but otherwise the species are allopatric (although *lugubris* and *flavescens* very closely approach each other in eastern Paraguay). The taxonomy followed is that of Short (1972b). *Celeus lugubris* is characterized by chestnut to rufous barred secondaries, rufous-chestnut upper tail coverts, and sooty, often rufous-tinged black underparts. *Celeus flavescens* is black below, or somewhat sooty black, with white barred secondaries and black or black and white upper tail coverts. Both *flavescens* and *lugubris* have dusky white to black bills. *Celeus elegans* is rufous-chestnut above and below, with no bars below and usually obscure dorsal barring; the bill is pale horn-colored. *Celeus castaneus* is smaller than the other species, pale-billed, rusty-cinnamon above and below, and finely black-banded dorsally and ventrally. They resemble one another in their pale rump patch, details of bill structure, pale yellowish or white stripe along the sides, and in other features (Short, 1972b).

Ecology. Arboreal, ant-foraging, nesting in cavities excavated in trees or in arboreal ant and termite nests. Nonmigratory. The species occurs in dry woodland, mainly in the northern chaco.

Distribution and variation. Endemic in central South America. It occurs from central-eastern Bolivia and west-central Mato Grosso S through the chaco and pantanal of western Paraguay, and the western part of eastern Paraguay to eastern Formosa, eastern Chaco and western Corrientes. A southern race, *kerri*, is slightly larger and blacker than northern *lugubris*. *Celeus flavescens kerri* occurs from southwestern Mato Grosso and the central-northern part of western Paraguay southward. The chaco is occupied by

one race or the other except for the western and central Argentine chaco. *Celeus lugubris kerri* extends beyond the chaco slightly to the E in Corrientes and eastern Paraguay, and *C. l. lugubris* extends beyond it to the N and NE (central Bolivia to west-central Mato Grosso). Thus, the warmer northern and more moist eastern chaco woodlands and most of the pantanal region are inhabited by this species.

Dryocopus lineatus
Lineated Woodpecker and
Dryocopus schulzi
Black-bodied Woodpecker
Figure 37

Taxonomy. *Dryocopus lineatus* is polytypic, *D. schulzi* is monotypic. These essentially allopatric species form a superspecies with *D. pileatus* of the Nearctic. The latter is large and black below, but otherwise closely resembles *D. lineatus* in habits and vocalizations (Short, in prep.). *Dryocopus lineatus* is barred white or buff-white and black ventrally, but otherwise is patterned like *pileatus*. *Dryocopus schulzi* is somewhat smaller than *lineatus*, and it is unbarred black below, with a black patch under the "wrist" of the wing. The three species are allopatric except for apparent contact between *schulzi* and *lineatus* in eastern Chaco Province, Argentina, where they may hybridize to some extent (*D. schulzi* "major" is likely to prove a hybrid of these two species).

Ecology. *Dryocopus lineatus* is a forest, forest edge, forest clearing, woodland, and savanna species. I have observed it nesting in one of a ring of small trees around a corral at a ranch in upland grassland a half-mile from woodland in northeastern Corrientes, and it visits isolated trees in cleared areas. Forages in trees for insects, often by scaling bark from dead trees or stubs (Short, 1970). *Dryocopus schulzi* seems restricted to dry chaco woodland. Its habits are unknown.

Distribution and variation. *Dryocopus lineatus* occurs from Mexico to northern Argentina, and *D. schulzi* is endemic in central South America. In South America *lineatus* is found S to northwestern Peru, and, in the E, throughout the lowlands (apparently not in the northeastern corner of Brazil, however) S to northern and far-

eastern Bolivia, eastern Paraguay, eastern Chaco Province and Corrientes, Argentina, and Rio Grande do Sul; an apparently isolated population occurs in Salta and adjacent southern Bolivia. *Dryocopus schulzi* occurs from the central Paraguayan chaco SW to Tucumán, S beyond the chaco slightly into Córdoba, and SE to eastern Chaco Province. It is lacking in the northern chaco (northern Paraguay, Bolivia, Mato Grosso), and apparently in much of the pantanal of the eastern chaco. The white-striped (scapular stripes) or *shiptoni* morph of *D. schulzi* occurs

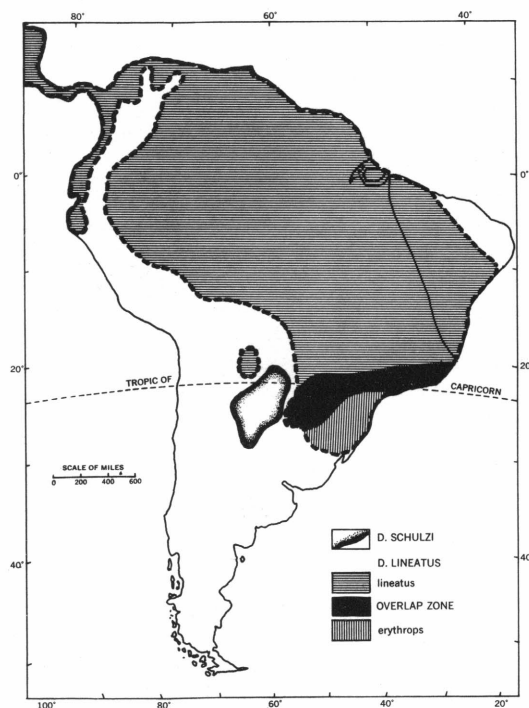


FIG. 37. Range of Lineated Woodpecker (*Dryocopus lineatus*) and Black-bodied Woodpecker (*D. schulzi*). These allospecies (a third occurs in North America) are forest and woodland birds; *schulzi* is a chaco species reaching dry subtropical forest. They meet and may hybridize in southeastern chaco. Conspecific isolate of *D. l. lineatus* occurs west of chaco in dry subtropical forest. Southeastern Brazilian *D. l. erythroptus* occurs beyond range of *D. l. lineatus*, but overlaps broadly and is morph of *lineatus* in overlap zone. Line marks occurrence of another race of *D. lineatus* in northeastern Brazil.

throughout the range of the species, although it may be more common in the southwest. Two specimens of *D. s. "major"* from eastern Chaco may be hybrids of *schulzi* × *lineatus*. *Dryocopus lineatus* occurs in the chaco along the western fringes (Villa Montes, Bolivia; Salta), in the pantanal of the Mato Grosso chaco, and apparently in easternmost Chaco Province (my recent field work failed to disclose the presence of either *schulzi* or *lineatus* in northern Santa Fe, the Paraguay River region and lower Pilcomayo River of eastern Formosa, and northwestern and northern Corrientes near the Upper Parana River). *Dryocopus lineatus lineatus*, which occurs in the Mato Grosso chaco, and (disjunctly) in Salta and Tarija, extends throughout most of the South American range of *D. lineatus*, N to Colombia, Venezuela, the Guianas, and eastern Peru, E to Goiás and Minas Gerais. This form is more finely barred below than more northern races, and its white bars are whiter (less buffy). From Rio de Janeiro W to central eastern Paraguay and S to western Paraná and eastern Chaco Province it occurs sympatrically with *D. "erythroptus"* which in this region simply represents a black-backed (it lacks the white scapular stripes typical of *D. lineatus*) morph of *D. l. lineatus*. Farther SE, in eastern São Paulo, Santa Catarina, and Rio Grande do Sul, *erythroptus* occurs as a race of *D. lineatus*, that is, the white-striped morph is lacking.

Campephilus melanoleucos
Crimson-crested Woodpecker

Taxonomy. Polytypic. With Middle American *guatemalensis* and western Ecuador-western Peruvian *gayaquilensis*, *C. melanoleucos* forms a superspecies. *Campephilus guatemalensis* is slightly larger, with a redder and blacker, less white head than the others; males lack white on the head and have a red throat, and a small (or no) black and white cheek patch, and females lack white on the face, have red reaching the bill, and a red and black forehead. *Campephilus melanoleucos* is smaller, the male shows white at the bill base, a black and white cheek patch and black throat, and the female has a white forehead and malar area and red behind the eyes. *Campephilus gayaquilensis* is like *melanoleucos* but has a browner overall tone, the male has red to the

bill at the malar and forehead and no white in that region, and the female has a redder head (no black on crown, red around eye and to bill above). The last species is allopatric, but *melanoleucos* and *guatemalensis* seem barely to meet in Panama, although they have not been seen together at the same locality (Wetmore, 1968).

Ecology. A large, wood-boring species, excavating for beetle larvae, ants, and other foods, and inhabiting forests and woodlands, and gallery forests in savannas. Nonmigratory.

Distribution and variation. Eastern Panama and South America, in the W to southern Colombia, and in the E throughout the lowlands to Ceará, the Brazilian highlands, São Paulo, eastern Paraguay, Corrientes, the northern chaco, and Salta, Argentina. *Campephilus melanoleucos albirostris*, a weakly differentiated form, occupies the northern fringe of the chaco in the pantanal of Mato Grosso, along the Paraguay River including the western bank in Paraguay and certainly in Santa Cruz, Bolivia, and possibly in the western and northern fringes of the Paraguayan chaco and in Salta. It extends beyond the chaco to Corrientes, eastern Paraguay, and N to eastern Bolivia, central Mato Grosso, and Bahía.

Campephilus leucopogon
Cream-backed Woodpecker

Taxonomy. Polytypic. Somewhat closely related to the *C. melanoleucos* complex, which it essentially replaces in the chaco.

Ecology. Habits as *melanoleucos*, but frequents chaco woodlands.

Distribution and variation. Endemic, essentially, in the chaco of South America. Occurs from the Bolivian chaco, the Paraguayan chaco uncommonly to the pantanal along the Paraguay River, and the Argentine chaco, extending beyond it slightly to the W (dry subtropical forest to some extent), SW (La Rioja), S (Córdoba), and E (to Entre Ríos and immediately adjacent Uruguay and southwestern Rio Grande do Sul). It does not occur in the Mato Grosso chaco. It almost exactly replaces *C. melanoleucos* in northwestern Corrientes (a few km. apart), and doubtless elsewhere at the fringes of the chaco. Birds from Salta, Jujuy, and Tucumán are somewhat larger than birds to the E and S, and have been separated as *C. l. major*; this form probably oc-

curs in the western fringes of the Argentine chaco, intergrading there with *leucopogon*.

FAMILY DENDROCOLAPTIDAE

Sittasomus griseicapillus
Olivaceous Woodcreeper

Taxonomy. Polytypic species, monotypic genus.

Ecology. Nonmigratory, bark-creeping; inhabits forests and savannas.

Distribution and variation. New World, Mexico to Argentina. In South America to northwestern Peru, and in E throughout the lowlands to Tucumán, Santiago del Estero, Santa Fe, Corrientes, and Rio Grande do Sul. Of the many races, *griseicapillus* is found in the southwestern portion of the species' range from Central Mato Grosso and eastern Bolivia S along the Andes to Tucumán, and E through Paraguay to eastern Paraguay (in the northwest), and then S along the Paraguay-Parana rivers to northern Santa Fe. It occurs throughout the chaco, except perhaps for the central Argentine portion, and beyond the chaco especially to the N.

Drymornis bridgesi
Scimitar-billed Woodcreeper

Taxonomy. Monotypic genus and species.

Ecology. A large and rather heavy-billed, curved-billed woodcreeper that feeds on insects on the ground about the bases of trees. Nests in trees, territorial, nonmigratory. Found in chaco woodlands.

Distribution. Endemic in south-central South America, centered in the southern chaco. Occurs from southernmost Bolivia and the Paraguayan chaco S through the chaco and dry subtropical forest along the Andes to Mendoza, La Pampa, and western Buenos Aires, and in the E to Entre Ríos and western Uruguay. Except for the dry subtropical forest, its distribution is mainly in the chaco and its southern and eastern chaco scrub extensions.

Xiphocolaptes major
Great Rufous Woodcreeper

Taxonomy. Polytypic. The species of *Xiphocolaptes* in South America are essentially all allo-

patric, and their status is uncertain; some may be conspecific, others may form a superspecies.

Ecology. An open woodland and edge species feeding in trees, bushes, and to some extent on the ground. Nonmigratory. Found in chaco woodlands, and savanna woods.

Distribution and variation. Endemic in central South America, from north-central Bolivia to western Mato Grosso and S through the chaco and dry subtropical forest to Santiago del Estero, Córdoba, and Santa Fe. Several rather weakly defined races are recognized, based upon tone of color of the body, especially the crown. The rusty *X. m. major* occupies the southern part of the species' range from Salta and northern Paraguay southward. Along the western fringe of the chaco and in the Bolivian chaco other races (more chestnut in color) occur. The species occupies the entire chaco except that portion E of the Parana River, and it extends beyond the chaco slightly to the W, and mainly to the N and NW.

Dendrocolaptes picumnus
Black-banded Woodcreeper and
Dendrocolaptes platyrostris
Planalto Woodcreeper

Taxonomy. Both species polytypic. These species replace each other geographically and resemble each other closely in size, bill proportions, and color pattern. They are not known to meet, although their ranges approach closely. *Dendrocolaptes picumnus* is paler throughout, and rustier; *D. platyrostris* is darker, brown, and less rusty overall, with blackish in the crown. The latter also has a darker bill, that of *picumnus* being pale (horn) in color.

Ecology. Large, tree-creeping, probing, and gleaning woodcreepers. *Dendrocolaptes picumnus* is a forest and woodland species, and *platyrostris* occupies forests, including gallery forests in the campo region. Insectivorous, territorial, nonmigratory.

Distribution. *Dendrocolaptes picumnus* occurs widely in Middle America and in South America (northern Colombia and lowlands E of Andes, E through Venezuela and Guianas, and S through all of Amazonia and western Pará to northern and eastern Bolivia, the western edge of Mato Grosso, the Paraguayan chaco, and the sub-Andean forests S to Tucumán). *Dendro-*

colaptes platyrostris is endemic in east-central South America, in the campo and caatinga region and through the southeastern Brazilian forests (southern Maranhão and Ceará S through eastern Mato Grosso and all southern Brazil to eastern Paraguay, eastern Chaco Province, Corrientes, and Rio Grande do Sul) to the eastern fringe of the chaco. The two may meet in southern Mato Grosso. The chaco is occupied by *D. picumnus pallescens* in the N (its range is entirely in the chaco of Paraguay, southwestern Mato Grosso, and eastern Bolivia), and by *D. platyrostris platyrostris* in eastern Formosa and eastern Chaco (gallery forest along Paraguay-Parana rivers, and thence up the Upper Parana River to Misiones and E). The latter race extends throughout eastern Paraguay and from Rio Grande do Sul to Minas Gerais and southern Bahía. It is darker than the other form from farther N. *Dendrocolaptes picumnus pallescens* is a well-marked, pale race with narrow buffy shaft streaks. The darker *D. picumnus casaresi* may occur in the western fringes of the Argentine chaco (neither species occurs in most of the Argentine chaco).

Lepidocolaptes angustirostris
Narrow-billed Woodcreeper

Taxonomy. Polytypic. Relationships in the genus are unclear.

Ecology. A small woodcreeper of woodland, woodland edges, savannas, and brushy parts of the pampas. Nonmigratory.

Distribution. Endemic in east-central South America. Occurs from the mouth of the Amazon and Ceará S through the campo region to Minas Gerais, western São Paulo, southwestern Rio Grande do Sul, and Uruguay, and W to Buenos Aires and Mendoza in the S, and Tucumán, Jujuy, and eastern and northern Bolivia. The entire chaco is inhabited by this species, with no less than three subspecies occurring in it. These are the weakly defined (slight color and size differences) *angustirostris* from eastern Formosa and eastern Chaco through northern Corrientes, Misiones, and eastern Paraguay to southern Mato Grosso, including the chaco portion; *dabbenei* from Salta and the Pilcomayo River area S through the chaco to Santa Fe, Córdoba, and La Rioja, and W to the dry subtropical forest; and *certhiolus* from northern Salta through central

Bolivia and the Paraguayan chaco to eastern Bolivia. These three races plus *praedatus* SE of the chaco and *hellmayri* of Andean Bolivia comprise the *angustirostris* group, which differs from the rufous-backed, plain-bellied northeastern *bivittatus* group in being darker-backed, with streaks and wavy bars ventrally. These groups interbreed in apparently secondary contact from northern Bolivia to southeastern Mato Grosso and Paraná.

Campylorhamphus trochilirostris
Red-billed Scythebill
Figure 38

Taxonomy. Polytypic. Forms a superspecies with *C. falcularius* of Espírito Santo to eastern Paraguay, Misiones, and Rio Grande do Sul. These may meet in northeastern Paraguay or Paraná. *Campylorhamphus trochilirostris* is paler in color, more rufous, with a pale (reddish) bill, whereas *falcularius*, often merged in *trochilirostris* (but differing from it much more than other, varied races of the latter), is darker overall, olive-backed, and black-billed.

Ecology. Forages on tree bark, probing into crevices and flipping insects back to the base of the bill (its tongue is short in contrast with its bill). Inhabits forest, woodlands, campos, and savannas. Nonmigratory, territorial.

Distribution and variation. The superspecies is mainly South American. *Campylorhamphus trochilirostris* occurs from eastern Panama S to Peru in the W, and through northern Colombia to Venezuela, and then S through western Amazonia (E along Amazon River to Pará) including eastern Peru and northern Bolivia, to Mato Grosso and NE to Ceará and Bahía, E to Minas Gerais and Paraná, S through eastern Bolivia, and western and central Paraguay, to La Rioja, Santa Fe, Entre Ríos, and northwestern Corrientes. Two moderately distinct races inhabit the chaco: *hellmayri* from the Paraguay-Argentine border in the W and central Paraguay (near the Paraguay River) S beyond the chaco to La Rioja, and to Santiago del Estero and Santa Fe, and E of the Parana River to Entre Ríos, western Corrientes, and the southwestern corner of eastern Paraguay; and *lafresnayanus* in the northern chaco of western Paraguay and adjacent Bolivia, Santa Cruz, and Mato Grosso, and beyond the chaco somewhat to the W (dry subtropical forest along

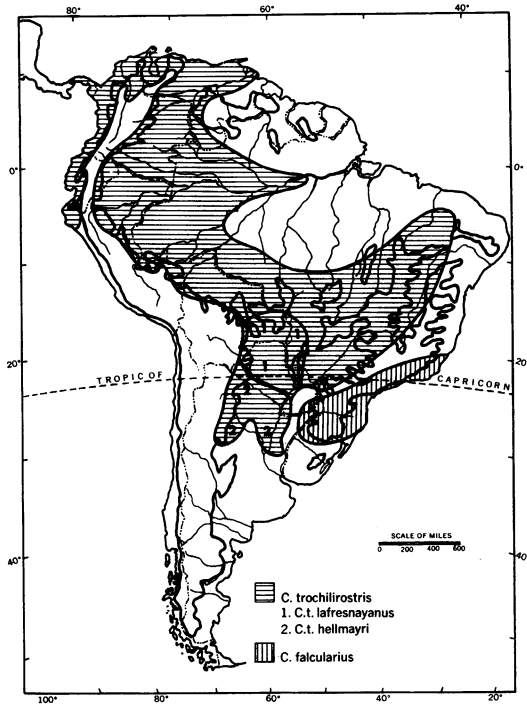


FIG. 38. Range of Red-billed Scythebill (*Campylorhamphus trochilirostris*) and its allo-species *C. falcularius*. The two do not appear to meet. Latter is forest species, former is widespread in forest, woodland, and scrub (caatinga, chaco). Two races of *trochilirostris* are largely confined to chaco.

Andes), and the N (northern Santa Cruz, central-western Mato Grosso). The southern form is larger, with a much longer bill than more northern *lafresnayanus*.

FAMILY FURNARIIDAE

Upucerthia certhioides Chaco Earthcreeper

Taxonomy. Polytypic. This species forms a superspecies with Andean slope *harterti* of central Bolivia. These species are related to essentially allopatric Andean *ruficauda* (Peru to southern Argentina in highlands), which is, however, larger, darker-tailed and somewhat differently patterned. *Upucerthia harterti* resembles the eastern race (*certhioides*, see below) of *certhioides*

rather than the adjacent race of that species, but its eye patch is darker and it has a pale abdomen.

Ecology. An inhabitant of woodland and brushlands, where it forages on the ground and low in bushes. Territorial, nesting in stick nests in bushes or trees. Nonmigratory.

Distribution and variation. The superspecies is endemic in central South America. *Upucerthia certhioides* occurs in the entire chaco except in the far N, where it is lacking (Mato Grosso, Santa Cruz), and S from the chaco to Mendoza, Córdoba, and Entre Ríos; it occurs also in the dry subtropical forest from La Rioja N to Tarija, Bolivia. Three races are recognized, the variation among them being largely nonclinal. *Upucerthia certhioides certhioides* occupies the more moist southeastern chaco, extending from eastern Formosa, eastern Chaco and Santa Fe into Entre Ríos and doubtless western Corrientes. This form is small, long-billed, and rufous in color. *Upucerthia certhioides estebani* occurs in the Paraguayan chaco, and the entire Argentine chaco W of *certhioides*, and it extends SW to San Luis (third race occurs farther SW). This form is larger, but short-billed, and browner and less rufous.

Furnarius rufus Rufous Hornero

Taxonomy. Polytypic. It is unclear which of the congeneric species is its closest relative.

Ecology. Common, territorial, vocal, frequents grasslands, savanna, woodland edges, cultivated lands, and clearings. Forages chiefly on ground, constructs distinctive mud nest in trees, or on fence posts. Nonmigratory.

Distribution and variation. Endemic in southern South America. Occurs from northern Bolivia across Mato Grosso to Bahía, and S through all of southern Brazil, eastern Bolivia, Paraguay, and Uruguay to La Rioja, Córdoba, Río Negro, and Buenos Aires. The species occupies all the chaco. Most of the chaco is inhabited by *F. r. paraguayae*, a form intermediate between Bolivian *commersoni* of the northern and eastern *badius* group, and distinctive *F. r. rufus* of Córdoba, Santa Fe, southern Chaco Province, Misiones and Paraná, and areas to the S. *Furnarius rufus rufus* is large, darker (browner) and less rufous above, and whiter and less rufous below than the *badius*

group. *Furnarius rufus paraguayae* is variable and intergradient between these groups, and is found from Tucumán, Chaco, and eastern Paraguay N through western Argentina to northern Paraguay and southwestern Mato Grosso.

Furnarius cristatus
Crested Hornero

Taxonomy. Monotypic. Relationships with other congeneric species are uncertain.

Ecology. A ground-foraging, woodland ovenbird, territorial and nonmigratory.

Distribution. Endemic in south-central South America, mainly in the chaco. Found in western Paraguay, the Argentine chaco, and Catamarca, La Rioja, Córdoba, and western Entre Ríos. Thus, it extends somewhat beyond the chaco to the S, the SW, and slightly beyond it to the W. It is absent from the Bolivian chaco, and from the pantanal between Mato Grosso and Chaco Province.

Leptasthenura platensis
Tufted Tit-spinetail

Taxonomy. Monotypic.

Ecology. A brushland ovenbird, foraging in trees and bushes, in which it nests. Found in the pampas, and the chaco woodlands. Nonmigratory.

Distribution. Endemic in southern South America. Occurs from the Paraguayan chaco S through the chaco and dry subtropical forest to La Rioja, La Pampa, Chubut, Buenos Aires, Uruguay, southern Rio Grande do Sul, and Entre Ríos. Thus, it occupies all of the chaco except the northern portion in Mato Grosso and Bolivia. It extends beyond the chaco through the pampas and southern chaco scrub to Patagonia.

Schoeniophylax phryganophila
Chotoy Spinetail

Taxonomy. Polytypic species, monotypic genus.

Ecology. Favors grassy areas with scattered bushes or open woodlands and woodland edges. Insectivorous, territorial, nonmigratory.

Distribution and variation. Endemic in south-central South America, from north-central

and eastern Bolivia, Mato Grosso, and western São Paulo SW through western and central Paraguay to Santiago del Estero, and from there SE through Corrientes and Entre Ríos to Uruguay and Rio Grande do Sul (*S. p. phryganophila*); apparently disjunct *petersi* occurs in Bahía and Minas Gerais. *Schoeniophylax phryganophila phryganophila* is larger and darker than *petersi*. The former subspecies inhabits the entire chaco, extending beyond it slightly to the E and W, and considerably farther NW, NE, and SE.

Synallaxis frontalis
Sooty-fronted Spinetail

Taxonomy. Polytypic. Forms a superspecies with central Andean (Peru to central Bolivia) *S. azarae*, and northern Andean (Colombia to Peru) *S. elegantior*. For the relationship of *elegantior* and *azarae* see Vaurie (1971); the former is paler than *azarae*, it lacks the ventral streaks shown by *azarae*, and has a different number of rectrices. *Synallaxis frontalis* resembles *azarae* but is smaller and darker.

Ecology. Inhabits forest-edge, woodland, and xeric scrub, also frequents bushy places in grasslands. Nonmigratory.

Distribution and variation. The superspecies is endemic in South America. The range of *frontalis* extends from Maranhão, Ceará, and Pernambuco SW through all of southern Brazil, Mato Grosso, eastern Bolivia, Paraguay, and Uruguay, and to Catamarca in western Argentina, and Santa Fe and Buenos Aires in eastern Argentina. The species is found in all parts of the chaco except the dry central chaco of Argentina. Of three weakly differentiated races, *frontalis* is the one occupying the chaco, although *fuscipennis* reaches the northwestern fringes of the chaco along the Bolivian-Paraguayan border (Steinbacher, 1968, reported an intermediate specimen from southwestern Paraguay).

Synallaxis albescens
Pale-breasted Spinetail

Taxonomy. Polytypic.

Ecology. Common in forest, forest-edge, and brushland. Insectivorous. Nonmigratory.

Distribution and variation. New World, Costa

Rica to northern Colombia, and over eastern South America E to Piauí and western Minas Gerais, and S, except for eastern Ecuador, to Mendoza, La Pampa, and Entre Ríos, Argentina, and western Santa Catarina and Rio Grande do Sul. Of the many races, *australis*, a rufescent form and the southernmost subspecies, occurs throughout the chaco, and beyond it to the S (in chaco scrub and monte as far as La Pampa), the W (dry subtropical forest), and to the E (to Corrientes).

Synallaxis scutatus
Ochre-cheeked Spinetail
Figure 39

Taxonomy. Polytypic. Its nearest relatives (*kollari*, *candei*) occur in northernmost Brazil, Colombia, and Venezuela. The genus *Poecilurus*, containing these three species, is merged in *Synallaxis* following Vaurie (1971).

Ecology. Little-known, found in forests, forest edges, and campos.

Distribution and variation. Endemic in central South America. Its range extends from Maranhão and Ceará to Bahía and São Paulo, then W to eastern Bolivia, and then S in the dry subtropical forest and adjacent chaco to Tucumán and western Chaco Province. *Synallaxis scutatus whitii* occurs from west-central Mato Grosso and eastern Bolivia to central Bolivia, then S to Tucumán and Chaco. It inhabits the fringes of the Argentine chaco in Salta and western Chaco, and probably in Santiago del Estero, and the Bolivian, and perhaps part of the Mato Grosso chaco as well. This race is brown-backed and less rufous overall than other races, but its wings are very rufous.

Certhiaxis pyrrhophia
Stripe-crowned Spinetail

Taxonomy. Polytypic. Relationships to other congeneric species are unclear.

Ecology. Somewhat woodcreeper-like, found in woodlands and brushy areas in savannas and pampas. Territorial, nonmigratory.

Distribution and variation. Endemic in south-central South America from northern and eastern Bolivia S through western Paraguay and

northern Argentina to Mendoza, Neuquén, and Río Negro, and E into Uruguay. Most of this range, that is from southern Bolivia and western Paraguay S, is occupied by the distinct *C. p. pyrrhophia*, a grayish race with gray-brown in the tail, which is entirely rufous in the other two forms. This race occupies all the chaco except in Mato Grosso and extends beyond the chaco W into the dry subtropical forest, S through chaco scrub and pampas to the fringe of Patagonia, and SE through the pampas to Uruguay.

Certhiaxis cinnamomea
Yellow-throated Spinetail

Taxonomy. Polytypic. Closely related to the partly sympatric *C. mustelina* of the Amazon Valley and eastern Peru.

Ecology. A spinetail of wet areas, including marshes, esteros, flooded grassland, and stream-side brush. Insectivorous, nonmigratory.

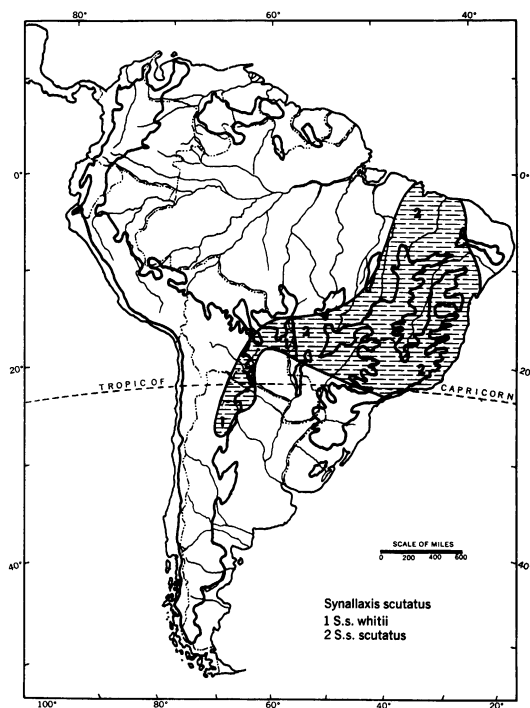


FIG. 39. Range of Ochre-cheeked Spinetail (*Synallaxis scutatus*). Species of caatinga region and adjacent areas that has race reaching northern and western edge of chaco.

Distribution and variation. Endemic in South America from northern Colombia and northern Venezuela E through the Guianas and the lower Amazonia region of Brazil, then S through eastern Amazonia, northern and eastern Bolivia, Paraguay, central Brazil, and eastern Brazil to Salta, Santiago del Estero, Santa Fe, and northern Buenos Aires, and in the E to western Uruguay, western Rio Grande do Sul, Misiones, and São Paulo. Of the many races, the southernmost, *russeola*, a dull brown form with grayish flanks, is rather weakly defined. It occurs from Bolivia, Mato Grosso, and Bahía S, including suitable areas throughout the chaco.

Thripophaga baeri
Short-billed Canastero

Taxonomy. Polytypic. I consider Patagonian *pyrrholeuca*, occurring from central Chile and southern Buenos Aires to Santa Cruz, as a very closely related allospecies, comprising a superspecies with *baeri*. These share the same tail pattern, general coloration, and soft texture of the plumage. *Thripophaga pyrrholeuca* has a long, thin bill and a relatively longer tail, whereas *baeri* is shorter and heavier-billed, with a shorter tail, and duller, less rufous coloration. The two species barely overlap in southern Buenos Aires and northeastern Río Negro. *Asthenes* is merged in *Thripophaga* following Vaurie (1971).

Ecology. Somewhat parid-like in habits, gleaning insects from the bushes and trees in which it is found; territorial and unlike *pyrrholeuca*, is nonmigratory; constructs a stick nest in bushes. It occurs in woodlands, and brushy areas in pampas or desert.

Distribution and variation. The superspecies is endemic in southern South America. *Thripophaga baeri* inhabits the chaco and pampas from the Paraguayan chaco S through the Argentine chaco, the sub-Andean "monte" in the W, E to Corrientes, Uruguay, and adjacent Rio Grande do Sul, and SW to the edge of Río Negro, and Mendoza. Both the nominate race and *T. b. chacoensis* occupy parts of the chaco. The latter race differs from *baeri* in its smaller size, proportionally shorter tail, more rufous coloration, and whiter superciliaries. *Thripophaga baeri chacoensis* is known only from the Paraguayan chaco, and *baeri* occupies the southern chaco and beyond it to the W (slightly), the S, and the E.

Phacellodomus rufifrons
Rufous-fronted Thornbird and
Phacellodomus sibilatrix
Little Thornbird

Figure 40

Taxonomy. *P. rufifrons* is polytypic, and *sibilatrix*, monotypic. These thornbirds form a superspecies. *Phacellodomus sibilatrix* is similar to the smaller races of *rufifrons*, differing most from the adjacent and narrowly sympatric *P. r. sincipitalis*. *Phacellodomus sibilatrix* is smaller than *rufifrons*, with a shorter bill, and a bi-colored (rusty-sided, dark-centered) tail.

Ecology. Forages in bushes, low in trees, and on the ground, in forest edges, woodlands, savannas, and desert scrub. Territorial, nonmigratory, builds large stick nests in trees.

Distribution and variation. The superspecies is endemic to South America. *Phacellodomus sibilatrix* occurs in the southern chaco and northern pampas from western Paraguay, Salta, and Corrientes S to Córdoba, northern Buenos Aires and Entre Ríos. *Phacellodomus rufifrons* is found disjunctly in Venezuela, eastern Colombia, eastern Ecuador, and northeastern Peru, and from northern Bolivia, central Mato Grosso, and western Pernambuco S in dry subtropical forest to Catamarca, the Paraguayan chaco, northeastern Paraguay, São Paulo, and Minas Gerais. The two species narrowly overlap in the central Paraguayan chaco, and in the western fringe of the chaco in Salta and perhaps farther S. *Phacellodomus sibilatrix* occurs throughout the southern chaco and to the S. The western chaco fringe, and the entire northern chaco (Bolivia, northern Paraguay, Mato Grosso) is occupied by *P. rufifrons sincipitalis*, a well-differentiated race that is considerably larger, and more rufous (less brown) than the other subspecies. It occurs beyond the chaco in the dry subtropical forest of northwestern Argentina, and in northern and eastern Bolivia intergrading with other races in Mato Grosso.

Phacellodomus ruber
Greater Thornbird

Taxonomy. Monotypic. None of the other thornbirds seems particularly closely related to it.

Ecology. Insectivorous, arboreal, nests in large stick nests in trees. Nonmigratory.

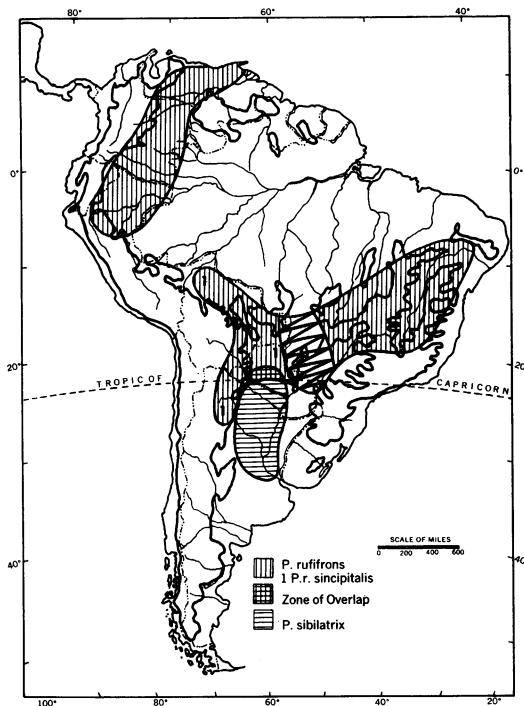


FIG. 40. Range of superspecies *Phacellodomus rufifrons*, including Rufous-fronted Thornbird (*P. rufifrons*) and Little Thornbird (*P. sibilatrix*). Latter is chaco bird that reaches northern pampas. *Phacellodomus rufifrons* has racially disjunct populations as shown. In the south it occurs in campo and caatinga, and westwardly a distinct form (*sincipitalis*) occupies northern chaco and adjacent Bolivia, Argentine dry subtropical forest, and southwestern campo. Intergradation is indicated between *sincipitalis* and other races (see text).

Distribution. Endemic in central South America from north-central and eastern Bolivia, Mato Grosso, and Bahía S and SW through Paraguay to Tucumán, Santa Fe, and northern Buenos Aires. It occurs throughout the chaco, slightly beyond it to the W, S, and E, and far to the N.

Phacellodomus striaticollis
Freckle-breasted Thornbird

Taxonomy. Polytypic. Relationships not clear with other congeners.

Ecology. A forest-edge and brushland thornbird, little known.

Distribution and variation. Endemic in south-central South America. Disjunct and well-marked races occur in eastern Bolivia to Tucumán (*maculipectus*), and from western Paraná, Misiones, Corrientes, and eastern Formosa S to northern Buenos Aires, Uruguay, and southern Rio Grande do Sul (*striaticollis*). *Phacellodomus striaticollis maculipectus* probably occurs in the chaco of Santa Cruz and elsewhere along the northwestern fringe of the chaco; it occurs also in western Santiago del Estero, but its status there is not certain. *Phacellodomus striaticollis striaticollis* ranges E from the southeastern chaco (eastern Formosa, eastern Chaco, Santa Fe). The latter race differs from *maculipectus* in its paler overall color, slightly larger size, less bright crown lacking white shaft streaks in front, weaker eye stripe, plain white (rather than variegated) cheeks, and less rufous chest.

Phleocryptes melanops
Wren-like Rushbird

Taxonomy. Monotypic genus, polytypic species.

Ecology. Insectivorous, found in marshes, marsh grass, flooded grasslands, and pantanal. Constructs wrenlike nest in rushes. May be partly migratory in extreme S.

Distribution and variation. Endemic in southern South America from coastal Peru, highland central Peru, central Bolivia, Paraguay, Rio Grande do Sul, and coastal Brazil N to Rio de Janeiro, S throughout lowlands and highlands in suitable situations to south-central Chile and Tierra del Fuego. Of the several races the small, short-billed *P. m. melanops* occupies a vast range from eastern Bolivia, Paraguay, northern Chile and Rio de Janeiro S to Tierra del Fuego. It occurs in suitable habitat within all the chaco except eastern Santa Cruz, Bolivia, and, apparently, the Mato Grosso pantanal, and extends to the E, W, and S from the chaco.

Anumbius annumbi
Firewood-gatherer

Taxonomy. Monotypic genus, polytypic species.

Ecology. Territorial ovenbird of open areas including pampas and woodland edges, as well as cultivated regions. One bush or tree in pampas

provides habitat for it, because it forages in grass and on the ground as well as in bushes. Builds large stick-nest in trees or bushes. Nonmigratory.

Distribution and variation. Endemic in southern South America. A disjunct population occurs in central Goiás; otherwise from the Paraguayan chaco, São Paulo, and Minas Gerais S to Chubut, Argentina. The disjunct northern isolate is *machrisi*, a weakly characterized race lacking most of the throat spots and apparently darker than the nominate race, which occurs in the rest of the species' range. The latter occupies the eastern chaco from Paraguay S through eastern Formosa, Chaco, and eastern Santiago del Estero to Santa Fe, and beyond to the S and E.

Coryphistera alaudina
Lark-like Brushrunner

Taxonomy. Monotypic genus and species.

Ecology. Ground-foraging, in brushy woodlands. It appears to migrate northward and eastward after breeding (Olrog, 1963).

Distribution. Endemic in southern South America, nesting from Tucumán, Chaco, and Entre Ríos S to Mendoza and La Pampa, in the chaco, the chaco scrub extension to the S, and xeric brushland (monte) in the W. It occurs in the southern chaco and from there S.

Pseudoseisura cristata
Rufous-crested Cacholote
Figure 41

Taxonomy. Polytypic. Not extremely closely related to its congeners.

Ecology. Little-known, occupies dry woodland, woodland edges, and caatinga. Nonmigratory.

Distribution and variation. Endemic in central South America. Disjunct populations occur in north-central and eastern Bolivia, western Mato Grosso, and the Paraguayan chaco (*unirufa*), and in Piauí and Pernambuco S to Minas Gerais and Bahía (*cristata*). *Pseudoseisura cristata unirufa* is slightly smaller and deeper cinnamon-rufous in color than *cristata*, with a shorter, more slender bill. It inhabits the northern chaco of Paraguay, Mato Grosso, and Bolivia, and extends to the NW from there.



FIG. 41. Range of Rufous-crested Cacholote (*Pseudoseisura cristata*), shown with lines, and Stripe-capped Sparrow (*Aimophila strigiceps*), shown stippled. Disjunctions involve races in each case, caatinga and northern chaco-campo edge form in *P. cristata*, and southeastern chaco and dry subtropical scrub form in *A. strigiceps*.

Pseudoseisura lophotes
Brown Cacholote

Taxonomy. Polytypic. No very close relatives in *Pseudoseisura*.

Ecology. Forages on the ground and in trees in brushland, and woodland. Partly migratory.

Distribution and variation. Endemic in south-central South America, with its range centering in the chaco and "monte"; occurring from eastern Bolivia S through the chaco and monte to Mendoza, Córdoba, Santa Fe, Entre Ríos, Uruguay, Rio Grande do Sul, and Corrientes. All the chaco is inhabited except in Mato Grosso. Two weakly defined races are recognized, including the darker, southern *argentina* in most of the species' range, and nominate *lophotes* in eastern Bolivia (Parkes, 1960).

Philydor rufosuperciliatus
Buff-browed Foliage-gleaner

Taxonomy. Polytypic. A relative of partly sympatric *P. subalaris*.

Ecology. Creeps and gleans insects in forests and forest edges, nonmigratory.

Distribution and variation. Endemic in central South America. A disjunct population occurs in central-northwestern Peru, otherwise from eastern Peru SE along the Andes through Bolivia to La Rioja in the W, and, probably disjunctly, from the eastern Paraguayan chaco, eastern Paraguay, Misiones, Rio Grande do Sul, and coastal Brazil from Rio de Janeiro S to northern Buenos Aires and Uruguay. It seems unreported for most of the Paraguayan chaco and easternmost Bolivia, hence a gap occurs between western and eastern populations. The eastern form, *acritus*, is less brown and more green-olive above and more olive below than other races; it is slightly smaller with a shorter bill. This race occurs in the pantanal riparian woods and eastern moist chaco woodland from northern Paraguay to Santa Fe, and from there E and S. The western chaco fringe is reached by western *oleagineus* of the sub-Andean forests.

FAMILY FORMICARIIDAE

Batara cinerea
Giant Antshrike

Taxonomy. Monotypic genus, polytypic species.

Ecology. Forages in forests and woodlands, mainly for insects but also small vertebrates. Nonmigratory. Territorial.

Distribution and variation. Endemic in central South America. Disjunct populations occur in eastern Bolivia SW through the western Paraguayan chaco and adjacent Bolivia to Tucumán, and in eastern Paraguay, Misiones, and Rio Grande do Sul NE to Espírito Santo. This antshrike is found in the chaco only in northwestern Paraguay, in the Argentine fringes of the chaco, Salta (both *B. c. argentina*), and in Santa Cruz, Bolivia (*excubitor*). *Batara cinerea argentina* differs from the other two races in its smaller size, more banded wings and tail, and the more ochraceous head of females.

Taraba major
Great Antshrike

Taxonomy. Polytypic. Monotypic genus.

Ecology. Frequents undergrowth and shrubbery of forests, woodlands, and more wooded parts of savannas, foraging primarily for insects. Nonmigratory.

Distribution and variation. Middle America and South America, S in W to northwestern Peru, and throughout the eastern lowlands to Tucumán, Entre Ríos, northwestern Uruguay, southwestern Rio Grande do Sul, western São Paulo, and Minas Gerais. *Taraba major major*, a weak race (female palest rufous of all races), occurs throughout the chaco, and beyond it slightly to the S (Córdoba), the W (Andean dry subtropical forest), the NW (northern Bolivia), the N (northern Mato Grosso), the NE (Goiás), and the E (Uruguay, eastern Paraguay, São Paulo).

Thamnophilus doliatus
Barred Antshrike

Taxonomy. Polytypic. No very close congeneric relative.

Ecology. Found in forest and woodland, occurring in savannas as well. Forages for insects low in thickets and tangles, often at forest edges. Nonmigratory.

Distribution and variation. Mexico to northwestern Argentina; in South America from Colombia to northwestern Peru, and in the E, throughout the lowlands to Paraguay, Salta, eastern Formosa, São Paulo, Minas Gerais, and Pernambuco. A rather weak race, *radiatus* (narrower ventral black bars than other races), occurs from eastern Bolivia, central Mato Grosso, and western São Paulo S through Paraguay and southeastern Bolivia to the Salta, Argentina, border, and Formosa. Thus, this race inhabits the northern chaco and extends beyond it to the N.

Thamnophilus caerulescens
Variable Antshrike
Figure 42

Taxonomy. Strongly polytypic and polymorphic. This species forms a superspecies with *T. amazonicus*, a longer-billed species in which the female is more rufous-headed. The latter spe-

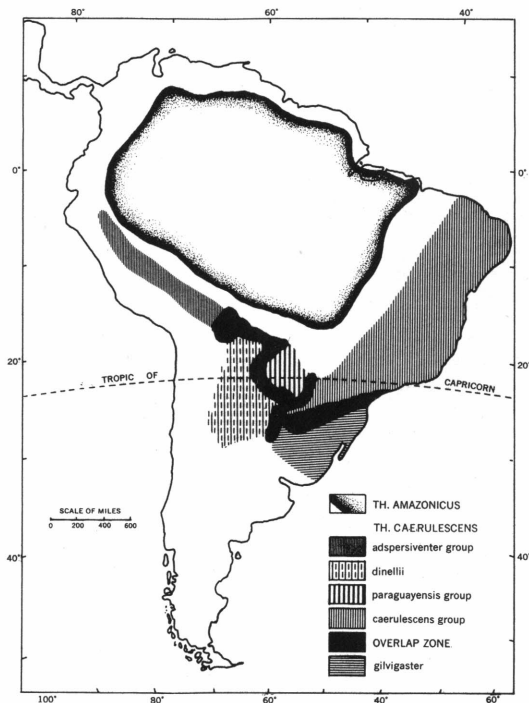


FIG. 42. Range of Variable Antshrike (*Thamnophilus caerulescens*) and its allospecies *T. amazonicus*. These species are not known to meet. *Thamnophilus amazonicus* is strictly Amazonian, whereas *caerulescens* occurs in forest and scrublands south of it, including chaco. Black areas within range of *caerulescens* indicate intergradation (or hybridization) among racial groups, of which there are five. Two groups occur in chaco. Subspecies *gilvigaster* overlaps with *caerulescens* of *caerulescens* subspecies group, the two forms acting as morphs in same way, and in almost same area as in *Dryocopus lineatus* (see fig. 37 and text).

cies occurs throughout Amazonia from southern Venezuela, eastern Colombia, eastern Ecuador, eastern Peru, and northern Bolivia, to central Mato Grosso, Maranhão, and the Guianas. The two species probably meet in Peru or Bolivia.

Ecology. An insectivorous forager in undergrowth in both humid and dry forests and woodlands, including the chaco. Nonmigratory.

Distribution and variation. The superspecies is endemic in South America. *Thamnophilus caerulescens* occurs from Andean and sub-Andean northern Peru along the Andes to central and

eastern Bolivia, from there E across Paraguay and southern Mato Grosso to Goiás, Ceará, and Pernambuco, and S to Catamarca, Córdoba, Entre Ríos, and Uruguay. This range includes the upland Peruvian and Bolivian *adspersiventer* group which intergrades with southern Bolivian and Argentine chaco *dinellii* in central Bolivia, and with *paraguayensis* (Paraguay except in SE; also in adjacent Mato Grosso), and the *caerulescens* group of eastern Brazil, which overlaps with the partly allopatric *gilvigaster* from Corrientes to São Paulo (the latter form is hence a "morph" in the overlap zone). The races *dinellii* and *paraguayensis* occupy the entire chaco, the former in Argentina, where it also frequents dry subtropical forest from Jujuy to Catamarca, and the latter in the Paraguayan chaco, the pantanal of Mato Grosso and (probably) the chaco of Santa Cruz. *Thamnophilus caerulescens dinellii* is (males) pale gray above with rufous over most of the underparts (much less dark gray than eastern *gilvigaster*), and *paraguayensis* is distinct by virtue of its white underparts and pale gray upperparts.

?Thamnophilus ruficapillus
Rufous-capped Antshrike

Taxonomy. Polytypic. Forms a superspecies with Andean *marcapatae* (disjunct populations of latter in northern and in southeastern Peru). *Thamnophilus marcapatae* is darker, grayer, and less pale rufescent than *ruficapillus*, and females are very dark (rufous) below, not whitish-buff as in *ruficapillus*.

Ecology. Found in forest undergrowth and in canopy. Nonmigratory.

Distribution and variation. The superspecies is endemic in central South America. *Thamnophilus ruficapillus* occurs from northern Bolivia S along the Andes to Tucumán, and, disjunctly, from Espírito Santo and eastern Paraguay S to northern Buenos Aires and Uruguay. It occurs outside of the chaco, but is very likely to reach the western fringes of the chaco in Salta or western Paraguay, and, in the E, it possibly may reach the W bank of the Parana River in the Santa Fe chaco. The eastern nominate *ruficapillus* is more rufous and less gray than the western races. Of the two western forms, *cochabambae* occurs from central Bolivia S, and is the one likely to occur in the western chaco fringes. It is lighter

gray and less fully barred below than is west-central Bolivian *subfasciatus*.

Myrmorchilus strigilatus
Stripe-backed Antbird
Figure 15

Taxonomy. Monotypic genus and species.

Ecology. Little-known, found in dry woodlands and caatinga. Nonmigratory.

Distribution. Endemic in South America. Two widely separated disjuncts, which have been racially named (the western *suspicax* is inseparable from eastern nominate *strigilatus* according to Naumburg, 1939), occur in southwestern Mato Grosso, eastern Bolivia, the Paraguayan chaco, Jujuy, Salta, and eastern Formosa, and in Paraíba and Ceará to Pernambuco and Bahía. The western population inhabits the entire northern chaco, and extends beyond the chaco only slightly to the W into dry subtropical forest and in the NE into the campo region from the pantanal of Mato Grosso. It does not occupy the southern chaco, including the dry central Argentine chaco.

Herpsilochmus pileatus
Black-capped Antwren
Figure 43

Taxonomy. Polytypic. Relationships are uncertain in *Herpsilochmus*.

Ecology. An insect-foraging inhabitant of dense undergrowth in forests, woodland, and savannas. Nonmigratory.

Distribution and variation. Endemic in South America. Disjunct populations occur in two areas of eastern (sub-Andean) Peru, and from Maranhão and Ceará SW through the caatinga and Brazilian highlands to Bahía, São Paulo, Mato Grosso, northeastern Paraguay, eastern Bolivia, western Paraguay, and Salta and Jujuy, Argentina. Most of the southern disjunct range (except for part of Bahía) is occupied by *H. p. atricapillus*, which has a longer tail, and a heavier, larger bill than Peruvian *motacilloides* or east-Brazilian *pileatus*, and it also has a white interscapular area. This form occurs in the northern chaco (northern Paraguayan chaco, Bolivia, Mato Grosso) and beyond it slightly to the W (dry sub-

tropical forest), and the N (Santa Cruz), and more extensively NE to Maranhão.

?*Formicivora rufa*
Rusty-backed Antwren

Taxonomy. Polytypic. Relationships not clear in *Formicivora*.

Ecology. Little-known, inhabits tangles and brushy areas in forest edges, caatinga, and savanna. Nonmigratory.

Distribution and variation. Endemic in central South America. Two isolated populations occur in eastern Peru; otherwise from northern Bolivia and Rondonia E across Mato Grosso to Minas Gerais and Paraíba, and from there NW through Maranhão to the lower Amazon region and Surinam, and S from Mato Grosso to eastern Paraguay. Nominate *rufa*, a pale-tailed, very rufous subspecies, occupies the southern part of

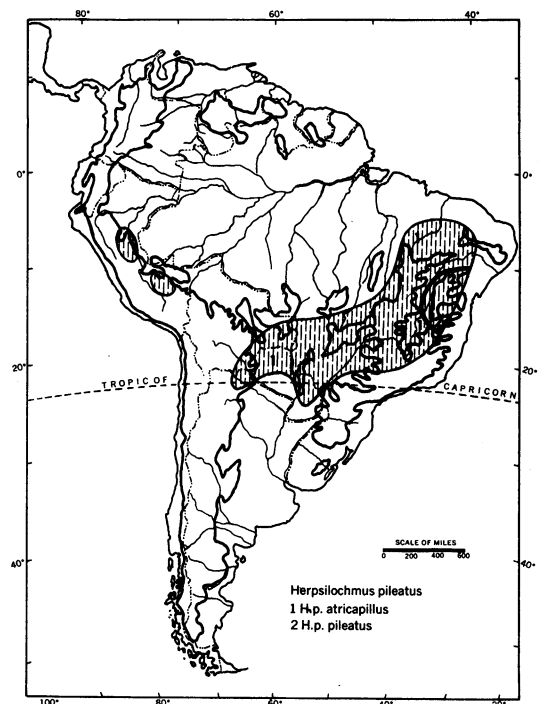


FIG. 43. Range of Black-capped Antwren (*Herpsilochmus pileatus*). Peruvian disjuncts form another subspecies, *motacilloides*. Species inhabits chaco-caatinga and reaches southern campo region.

the main range of the species, from northern Bolivia to Minas Gerais and S to eastern Bolivia, eastern Paraguay, and São Paulo. This race probably occurs in the Santa Cruz, Bolivia, and the pantanal of Mato Grosso parts of the chaco.

?Pyriglena leuconota
White-backed Fire-eye

Taxonomy. Polytypic. Forms a superspecies with *P. atra* of coastal Bahía, and *P. leucoptera* of eastern Paraguay and Misiones through southern Mato Grosso and Santa Catarina to western Bahía and Minas Gerais. These three species are very likely to prove conspecific, but this matter requires study, preferably in the field. *Pyriglena leuconota*, the only polytypic species, lacks the white present on the wings of *leucoptera*; females are darker than those of *leucoptera*, have white on their backs, a relatively long tail, and thin bill. *Pyriglena leucoptera* has white wing patches, females are paler than in *leuconota* and lack white in the back feathers. *Pyriglena atra* lacks white wing patches, females lack white in the back, proportionally the tail is short, and the bill is longer and heavier than in the others. As their ranges are allopatric and closely approach each other (*leucoptera-leuconota* in Mato Grosso, Pernambuco; *atra-leucoptera* in Bahía) without signs of interbreeding, and especially considering the interposition of *leucoptera* (and *atra*) partly between populations of *leuconota*, it seems best to treat these forms as species for the time being.

Ecology. Little-known foragers in dense vegetation in forests and caatinga. Nonmigratory.

Distribution and variation. The superspecies is endemic in South America. *Pyriglena leuconota* occurs from south-central Colombia, western Ecuador (both isolated populations), southeastern Colombia to eastern Peru, northern and eastern Bolivia and central Mato Grosso, and, disjunctly, the lower Amazon to Pernambuco along the northeastern Brazilian coast. *Pyriglena leuconota maura*, a rather weakly characterized form (females with pale cheeks and eye stripe present), occurs in eastern Bolivia and central Mato Grosso, probably including the chaco of Santa Cruz.

FAMILY RHINOCRYPTIDAE

Rhinocrypta lanceolata
Crested Gallito
Figure 20

Taxonomy. Monotypic genus and species.

Ecology. Frequents xeric brushland, forages on ground and in low bushes in the drier parts of the chaco, and in monte and chaco scrub.

Distribution. Endemic in south-central South America from the chaco of Santa Cruz, Bolivia, S through central western Paraguay, the central chaco of Argentina, and Tucumán S to Mendoza, Río Negro, and southwestern Buenos Aires. It is found throughout the dry central chaco from Santa Cruz, Bolivia, S to Santiago del Estero, where its range expands W into the monte, and S in the chaco scrub to southwestern Buenos Aires and Río Negro. It does not reach the pantanal or eastern edge of the moist chaco woodland S of northern Paraguay (Puerto Casado).

Melanopareia maximiliani
Olive-crowned Crescentchest

Taxonomy. Polytypic. *Melanopareia maximiliani* forms a superspecies with *M. torquata* of northeastern Bolivia and Pará E to Piauí and Bahía, and S to São Paulo. These two species differ from *M. elegans* and *M. maranonica* as follows: the tail is paler and concolored with the back; they lack a black cap; the white in the back is moderate to extensive; both have a small bill, similar in shape, but different from *elegans* and *maranonica*; and both have a reduced black and white wing pattern. *Melanopareia maximiliani* differs from *torquata* in its olive (versus rufous) upperparts, its darker ventral color, its lack of a rusty nape patch, its greater amount of white on the back, and in the presence of black around the white back patch. The two species replace each other geographically, and they may meet in Santa Cruz, Bolivia. The genus is of uncertain affinities, and I see no sense in removing it from the Formicariidae prematurely—indeed its habits and plumage pattern suggest formicariid affinities.

Ecology. A woodland and savanna species

found in brush and low shrubs, and foraging upon insects. Nonmigratory.

Distribution and variation. Genus endemic in South America. *Melanopareia maximiliani* occurs from La Paz, Bolivia, and, disjunctly, from eastern Bolivia S through western Paraguay to Catarmarca in the W, and to northern Santa Fe in the E; questionably occurs in Córdoba (possibly disjunctly). Two races are recognized, the nominate form in the yungas of La Paz, and *argentina*, a paler, dorsally grayer, ventrally less rufous form from Santa Cruz and Chuquisaca S. The latter race occurs in the chaco of Paraguay and Santa Cruz (not Mato Grosso), and the eastern and western Argentine chaco, but not (apparently) the arid central chaco of Argentina. It extends beyond the chaco slightly to the NW, the SW (in monte scrub), and probably the S (possibly Córdoba).

FAMILY COTINGIDAE

Attila phoenicurus
Rufous-tailed Attila
Figure 44

Taxonomy. Monotypic. Seems related to the *cinnamomeus* group of *Attila*, and certainly not generically separable (as monotypic *Pseudattila*). This genus probably belongs in the Tyrannidae.

Ecology. A foliage-foraging insectivorous bird of the canopy of woodlands and forests, also in campos. Possibly partly migratory.

Distribution. Endemic in South America, disjunctly in southern Venezuela (migrant or wintering?), in the central Amazon Valley, and in Mato Grosso and Goiás to Paraguay, Misiones, and Paraná. Within the chaco it occurs only in central western Paraguay and in the pantanal region of Mato Grosso. Thus, it extends from the northern chaco across Mato Grosso and to the NE.

Casiornis rufa
Rufous Casiornis

Taxonomy. Monotypic. Forms a superspecies with *C. fusca* of the northeastern corner of Brazil (from the lower Amazon and its mouth SE through Maranhão to Paraíba and Bahia). These

forms very likely will prove conspecific; *fusca* is browner above and yellower below. The lower Amazon and Maranhão records of *rufa* probably represent migrant individuals. Very likely *Casiornis* is a tyrannid genus.

Ecology. Flycatches in the tops of trees and shrubs, and nests in same sites. Partly migratory.

Distribution. The superspecies is endemic in South America. *Casiornis rufa* is found from southern Maranhão and Goiás S to Minas Gerais and São Paulo, and W through Mato Grosso to central and eastern Bolivia, western Paraguay, Salta, and Corrientes. It inhabits the entire northern chaco (western Paraguay, Santa Cruz, Mato Grosso), the western fringe of the Argentine chaco in Salta, and the eastern Argentine chaco

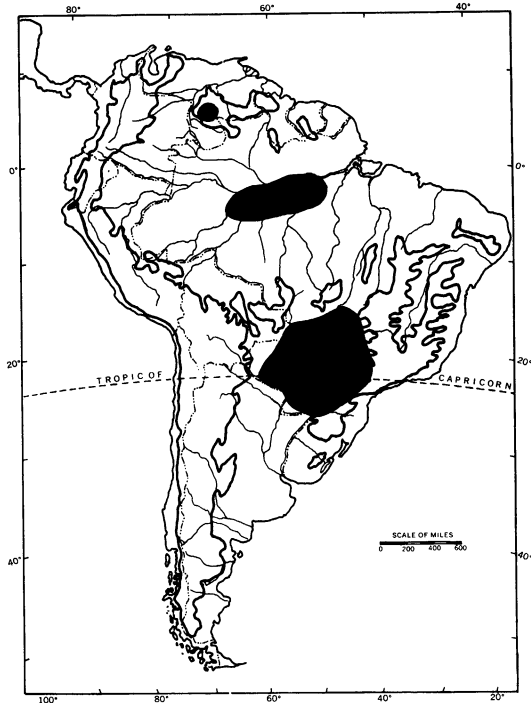


FIG. 44. Range of Rufous-tailed Attila (*Attila phoenicurus*). This monotypic, peculiarly distributed species of chaco-campo-southeastern Brazilian forest ecotone may be a migrant to northern areas shown here (otherwise one would expect differentiation, or a more widespread distribution, given different habitats in disjunct areas).

in eastern Formosa, eastern Chaco, and northwestern Corrientes. It extends beyond the chaco slightly to the W (dry subtropical forest), and extensively to the N and NE.

Xenopsaris albinucha
White-naped Xenopsaris
Figure 45

Taxonomy. Polytypic species, monotypic genus. No close relatives. Variously considered a tyrannid or a cotingid.

Ecology. Flycatches, often from a position low in a tree, bush, or even grass, at edges or openings in woodland or caatinga. Migratory in part.

Distribution and variation. Endemic in South America. Disjunct populations occur in western Venezuela and in eastern Venezuela (*X. a. minor*), and in the caatinga (Piauí, Ceará, Bahía) and the chaco and its fringes (nominate *albinucha*). The western disjunct population of *albinucha* occurs in northern Bolivia (Beni), and in western Paraguay S through Salta and the chaco, including western Corrientes and probably western Entre Ríos to Tucumán, Córdoba, and northern Buenos Aires. This population extends beyond the chaco slightly to the W, to the S, (mainly along the Parana River to Buenos Aires, and in chaco scrub in Córdoba) and to the N (Beni). It does not occur in Santa Cruz or Mato Grosso. The race *albinucha* is somewhat larger than *minor*, but resembles it in color. The caatinga birds do not differ from those of the chaco.

Pachyramphus viridis
Green-backed Becard

Taxonomy. Polytypic. It appears not to be especially closely related to any other congeneric species.

Ecology. Forages for insects in the canopy of forest and woodland trees. Nonmigratory.

Distribution and variation. Endemic in South America. Its range extends from eastern Ecuador, eastern Peru, southeastern Venezuela, and lower Amazon region (all of these disjunctly), and Piauí and Ceará S to Bahía and coastal Brazil to Rio Grande do Sul, and inland W through Goiás and Mato Grosso to eastern Bolivia, all of Para-

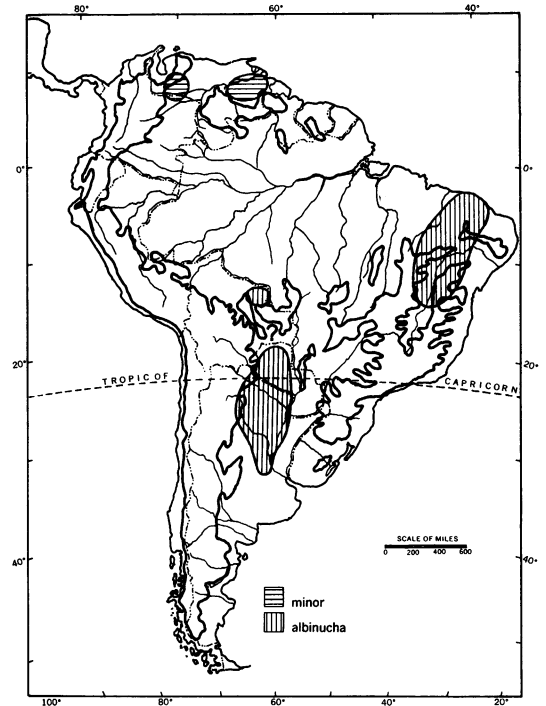


FIG. 45. Range of White-naped Xenopsaris (*Xenopsaris albinucha*). Northern disjunct isolates, racially distinct from those to the south, occupy less xeric areas than do southern disjuncts. Southern race is chaco-dry subtropical forest-caatinga form (isolate in Bolivia).

guay, northwestern Argentina (Jujuy and Salta to Tucumán), and northeastern Argentina northern Santa Fe, Formosa, eastern Chaco, Corrientes, Misiones). The entire southern range from Piauí S, plus the lower Amazon, is occupied by *P. v. viridis*, a distinct, gray-headed rather than green-headed, form having little black in the wings. This form occurs in the northern chaco, and in the southwestern chaco fringes (Salta to Tucumán), and the southeastern chaco (eastern Formosa, eastern Chaco, Corrientes). It extends slightly to the W of the chaco, and extensively to the E and NE.

Pachyramphus polychopterus
White-winged Becard

Taxonomy. Polytypic. Related to sympatric *marginatus* and *albogriseus*.

Ecology. Inhabits forest and woodland, for-

aging in the foliage. Nonmigratory. Builds a covered-over nest high in trees.

Distribution and variation. Middle America and South America. In South America from northern Colombia E and S throughout the lowlands (all countries) to Tucumán, northern Buenos Aires, and Uruguay. *Pachyramphus polychopterus spixii* occurs from northern Bolivia, eastern Bolivia, central Mato Grosso, and São Paulo S through Paraguay, southern Brazil, Uruguay, and northern Argentina. It is found throughout the chaco, and beyond it to the S (Córdoba, northern Buenos Aires), the W (dry subtropical forest), the E, and the N. This race is larger than those to the N, the male is very dark (gray) below, and the female has brown wings with narrow buff bars.

Platyparis rufus
Crested Becard

Taxonomy. Polytypic. A relative of the *P. minor* group and *P. niger* (Mayr and Short, 1970).

Ecology. Insectivorous, foliage-foraging, in forest edges, woodlands, and campos. Nonmigratory.

Distribution and variation. Endemic in South America, from eastern Peru, southern Amazonia, and the mouth of the Amazon S through northern and eastern Bolivia, all of southern Brazil (except the extreme eastern region), and Paraguay, to Tucumán in western Argentina, Santa Fe and Corrientes in eastern Argentina, and Rio Grande do Sul. A western, sub-Andean race *audax* (Peru, Bolivia, northwestern Argentina) is distinguished on the basis of minor color differences in males only (males darker above, and lacking a buffy wash below in comparison with nominate *rufus*). This form probably reaches the western fringes of the chaco. Otherwise, the chaco of Santa Cruz, Mato Grosso, western Paraguay, eastern Formosa, and eastern Chaco, and the areas to the E and N are occupied by *P. r. rufus*.

Tityra cayana
Black-tailed Tityra

Taxonomy. Polytypic. It has no very close congeneric relatives.

Ecology. A forest, woodland, and savanna

species requiring holes in dead trees in which to nest. Forages for larger insects, partly by fly-catching, in tree tops; also takes some fruits. Nonmigratory.

Distribution and variation. Endemic in South America from Venezuela S through eastern Ecuador, eastern Peru, the Guianas, all of Brazil to Rio Grande do Sul, northern and eastern Bolivia, central and eastern Paraguay, to Chaco and Misiones, Argentina. *Tityra cayana braziliensis* is the southern race (northern Bolivia, Mato Grosso, and Ceará S to the border of the species' range) found in the eastern chaco from Santa Cruz and the pantanal of Mato Grosso S through the eastern chaco of Paraguay (W to central-western Paraguay) to eastern Formosa and eastern Chaco, and beyond to the NW, the E (northern Corrientes, Misiones, eastern Paraguay), and NE. This race is larger than the two northern forms, the male is very pale, and the female is browner above with a more streaked, less solid blackish crown.

Tityra inquisitor
Black-crowned Tityra

Taxonomy. Polytypic. It has no close relatives.

Ecology. Frequents large trees at forest edges, forest clearings, and in savannas. Nests in holes in trees. Nonmigratory.

Distribution and variation. Middle and South America. It occurs S to Ecuador W of the Andes, and E of the Andes it inhabits lowlands (not in Guianan highlands) and the Brazilian planalto, from Venezuela through eastern Colombia, eastern Ecuador, eastern Peru, Amazonia, Surinam, the mouth of the Amazon, and all of central and southern Brazil to Rio Grande do Sul, Misiones, eastern Paraguay, eastern Formosa, and northern and eastern Bolivia. The more northern *T. i. pelzelni* occurs in the pantanal of Mato Grosso, Santa Cruz, and probably adjacent Paraguay, and from there NE through part of northern Bolivia and Mato Grosso and Goiás to the mouth of the Amazon. The more southern and eastern form, *inquisitor*, occurs in eastern Formosa and probably the pantanal of adjacent Paraguay, and from there E through Misiones and eastern Paraguay and coastal Brazil NE to Pernambuco and Ceará. The latter race is larger than

pelzelni, and the base of the tail has a more limited white area; both are black-cheeked subspecies.

FAMILY TYRANNIDAE

Xolmis cinerea Gray Monjita

Taxonomy. Polytypic. Forms a superspecies with *X. coronata*, which breeds from La Pampa and Buenos Aires S into northern Patagonia. These allopatric species have generally similar color patterns; e.g., both have a white-tipped black tail, and both have "scaloped" wing coverts. *Xolmis cinerea* is smaller than *coronata*, it lacks the crown patch and superciliary stripe of *coronata*, and its breast is gray, not white.

Ecology. Flycatches from trees, wires, fences, in forest clearings, about habitations, and in woodlands and savannas. Nonmigratory, although *coronata* is migratory.

Distribution and variation. The superspecies is endemic in South America. *Xolmis cinerea* occurs from the mouth of the Amazon, southern Amazonia, and northern Bolivia S throughout southern Brazil, eastern Bolivia, Paraguay, Uruguay, and Argentina S to Tucumán, Santa Fe, and northern Buenos Aires. A southwestern race, *pepoaza*, is paler (grayer, less brown) above, and less gray-breasted than the northern and eastern *cinerea*, and inhabits the entire chaco except possibly northwestern Paraguay, and it extends beyond the chaco to the W (very slightly into dry subtropical forest), the N (west-central Mato Grosso), the E (eastern Paraguay, Corrientes, Entre Ríos), and to the S (northern Buenos Aires).

Xolmis irupero White Monjita

Taxonomy. Polytypic. Not very closely related to any other species of *Xolmis*.

Ecology. Frequents woodland, brushland, and open country, often found about cultivated areas. It nests in crevices or holes in trees and fence posts. Nonmigratory.

Distribution and variation. Endemic in South America. Two rather weakly defined races are disjunct in the caatinga (*nivea*), and in the chaco

and northern pampas, and surrounding areas (*irupero*). *Xolmis irupero nivea*, which is slightly smaller-billed, with more black in its less-forked tail, occurs in Ceará, Bahía, and Pernambuco. *Xolmis irupero irupero* is found from northern Bolivia and western Mato Grosso S through all of Paraguay, Rio Grande do Sul, Uruguay, and Argentina as far as Mendoza, Córdoba, and Buenos Aires. The latter inhabits the entire chaco, and extends beyond it in all directions (W to dry subtropical forest, S to Mendoza, San Juan, and Buenos Aires, E to eastern Paraguay and Uruguay, and N to central Mato Grosso and northern Bolivia).

Xolmis dominicana Black and White Monjita

Taxonomy. Monotypic. Possibly related most closely to *irupero*.

Ecology. Uncommon, found in bushy growth in open country, and edges of gallery forest. Nonmigratory.

Distribution. Endemic in south-central South America, from Paraná and central Paraguay S especially along the Uruguay and Paraguay-Parana rivers, to northern Buenos Aires; W to the eastern chaco of Argentina, and E to coastal Rio Grande do Sul and Uruguay. Within the chaco it is confined to the southeastern pantanal area from eastern Formosa and probably adjacent western Paraguay S through eastern Chaco and Santa Fe. From there it extends NE, E, and SE.

Gubernetes yetapa Streamer-tailed Tyrant

Taxonomy. Monotypic genus and species, seemingly related to *Alectrurus* and perhaps to *Xolmis*.

Ecology. Occupies woodland edges and savannas, favoring the vicinity of wet areas, such as flooded savannas, irrigation channels. It occurs away from trees, as well as in woodland edges. Possibly migratory in extreme S.

Distribution. Endemic in central South America. It is found from northern Bolivia E through central Mato Grosso to Minas Gerais and Bahía, and S through eastern Bolivia, southern Mato Grosso and eastern Paraguay to Chaco, northern

Corrientes, and Misiones, Argentina, and São Paulo. This tyrant occupies the fringe of the chaco in eastern Chaco Province (possibly of regular occurrence), and probably in Santa Cruz, Bolivia, and the chaco of Mato Grosso. From there it extends E, NE, and NW to central-northern Bolivia.

?Alectrurus tricolor
Cock-tailed Tyrant

Taxonomy. Monotypic. Related to *A. risora* and probably *Gubernetes yetapa*.

Ecology. A forest clearing, woodland edge, and savanna species, foraging frequently near the ground. Nonmigratory.

Distribution. Endemic in east-central South America; distribution very like that of *Gubernetes yetapa*. Occurs from north-central Bolivia, central Mato Grosso and Espírito Santo S only to eastern Bolivia in the W and São Paulo in the E, but through eastern Paraguay to Corrientes in the central part of its range. It probably breeds in the chaco of Santa Cruz, Bolivia, and in the Mato Grosso chaco, but it is not known to do so.

Alectrurus risora
Strange-tailed Tyrant

Taxonomy. Monotypic. Usually treated as a monotypic genus (*Yetapa*), but its habits, bill, modified outer primary, and even its tail modification (under-tail coverts modified) seem to ally it with *A. tricolor*, which it generally resembles in plumage pattern.

Ecology. Found in woodland edge, savanna, and pampas, usually seen in bushes in more or less open country. Frequently found near water, in brush along streams. Presumably nonmigratory.

Distribution. Endemic in central South America. Found from western São Paulo and southern Mato Grosso S through central and eastern Paraguay to the eastern Argentine chaco, San Luis, and Buenos Aires, and in the E to Rio Grande do Sul and Uruguay. It occurs in the eastern chaco from the pantanal of Mato Grosso and the eastern Paraguayan chaco through Formosa and Chaco to Santa Fe, and beyond the chaco it extends to the E and S.

Knipolegus aterrimus
White-winged Black-tyrant

Taxonomy. Polytypic. It appears not to be related very closely to other congeneric species.

Ecology. In woodland and brushland and also in riparian growth in open country. At least the southern populations are migratory.

Distribution and variation. Endemic in South America, occurring along the eastern edge of the Andes from northern Peru to southern Bolivia, and from dry subtropical forest and chaco woodland to monte and Patagonian scrub vegetation S to Chubut, and E to Entre Ríos and Buenos Aires. Of the four races, the migratory *aterrimus* is found from north-central Bolivia S. This race is larger than northern subspecies, the male is blacker, the female is darker below and on the crown, females have cinnamon on the outer primary web, and also a different tail pattern than northern races. This form is found in the southern chaco from Salta and Santa Fe S, W into the dry subtropical forest, and S through chaco scrub to Patagonia.

Knipolegus cyanirostris
Blue-billed Black-tyrant and
?Knipolegus cabanisi
Plumbeous Tyrant

Taxonomy. Monotypic. These form a super-species. *Knipolegus cabanisi* resembles *K. cyanirostris* in bill structure, tail pattern, and the color pattern of females. It differs from *cyanirostris* in the replacement of black by gray in males, by its white patch in the primaries, by the less rufous coloration of females, and by its larger size.

Ecology. In forest-edge and woodland, and bushy areas of the northern pampas, often near water. Nonmigratory.

Distribution. The superspecies is endemic in central South America. *Knipolegus cyanirostris* is found from the eastern chaco of Paraguay and southern Mato Grosso E to Espírito Santo, and S through eastern Formosa, eastern Chaco Province, and northeastern Argentina to northern Buenos Aires; in the E occurs throughout southern Brazil and Uruguay. This species thus occupies the eastern chaco woodlands and pantanal from southernmost Mato Grosso to northern

Santa Fe, and S and E from there throughout the species' range. *Knipolegus cabanisi* may occur in the fringes of the western chaco (Salta; Santa Cruz, Bolivia).

Knipolegus striaticeps
Cinereous Tyrant

Taxonomy. Monotypic. This species appears too closely related to species of *Knipolegus* to form a monotypic genus (*Entotriccus*) of its own; it and "*Phaeotriccus*" are separated on the basis of narrowed outer primaries, a feature variable in tyrannids.

Ecology. Inhabits the chaco-like monte (desert scrub), and the fringes of the chaco. Migratory.

Distribution. Endemic in western Argentina. According to Olrog (1963) it breeds in a small area of Tucumán, Santiago del Estero, Catamarca, La Rioja, and Córdoba, and is a migrant N and E of there. Specimens from the Paraguayan chaco reported by Steinbacher (1962) were taken in October, and in January; this tyrant may breed in the drier parts of the Paraguayan chaco.¹ Otherwise, it occurs in the chaco only in southern Santiago del Estero.

Hymenops perspicillata
Spectacled Tyrant

Taxonomy. Polytypic. Genus monotypic.

Ecology. A flycatcher of reeds and grass in marshes, esteros, and flooded pampas. Territorial. Migratory.

Distribution and variation. Endemic in southern South America. Breeds from northern Chile to south-central Chile, and from Uruguay, Rio Grande do Sul, and approximately the Paraguayan border of Argentina S to Chubut. The eastern subspecies, *perspicillata* (smaller size, more white in wings), occurs from Río Negro and Neuquén N to eastern Formosa, Corrientes, and Rio Grande do Sul. This form is found in the eastern chaco of Argentina, especially in the pantanal, and W an unknown distance into the central Argentine chaco, doubtless only at suitably wet locations.

¹ Recently taken specimens (AMNH) from Lichtenau in the Paraguayan chaco include several January birds with greatly enlarged gonads; breeding definitely is indicated.

Fluvicola pica
Pied Water-tyrant
Figure 46

Taxonomy. Polytypic. Forms a superspecies with *F. nengeta*. The latter is very similar in plumage and bill structure to *pica*, which is blacker above, with reduced white in the tail and an almost obsolete eye-stripe. Both species have disjunct populations, curiously distributed in western Ecuador-northwestern Peru and in far-eastern coastal Brazil from Maranhão to Bahia, and Espírito Santo (*nengeta*), and in northern South America, and in the chaco region (*pica*).

Ecology. A flycatcher of esteros and marshes, usually about open water. Migratory.

Distribution and variation. The superspecies essentially is endemic to South America. *Fluvicola pica* occurs from eastern Panama and northern Colombia across Venezuela to the Guianas and S to southeastern Colombia and the northern edge of Brazil (*F. p. pica*), and from eastern Bolivia and southern Mato Grosso S through Paraguay to La Rioja, Santiago del Estero, northern Buenos Aires, and western Uruguay (*F. p. albiventer*). The latter race migrates northward to the Amazon River region, and southeastern Peru; its northern breeding limits are uncertain. This form is much larger than northern *pica*, its back lacks the white of *pica* and the rump is less white; it has been considered a distinct species, but I doubt that it is. This species occurs throughout the chaco in suitably wet places, and it occurs somewhat beyond the chaco to the NW, W, and SW, and, more extensively to the E and SE.

Fluvicola leucocephala
White-headed Marsh-tyrant

Taxonomy. Monotypic. This species in plumage pattern and form, as well as its habits, seems closely related to *Fluvicola pica* and *F. nengeta*. As the latter form a superspecies, it is not unduly stretching the generic concept to include *leucocephala* in *Fluvicola*; *leucocephala* has been treated as a monotypic genus (*Arundinicola*).

Ecology. Lives in sawgrass and reeds in esteros and marshes in both wet and dry regions. Possibly only a migrant in some parts of its northern range.

Distribution. Endemic in South America. Oc-

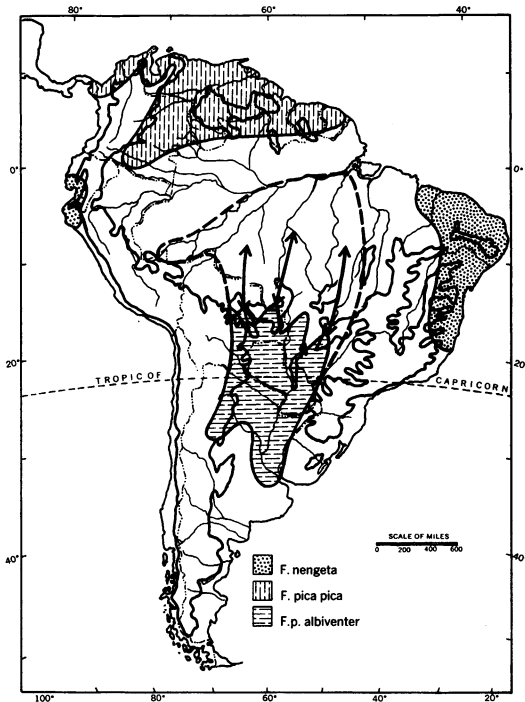


FIG. 46. Range of superspecies *Fluvicola nengeta*, including *F. nengeta* and the Pied Water-Tyrant, *F. pica*. *Fluvicola nengeta* occurs in widely disjunct xeric areas. Disjunct races of *F. pica* inhabit somewhat different environments, in part. Southern form frequents wet areas of chaco, wet pampas and adjacent dry subtropical forest and campo; it is partly migratory as indicated by arrows and dashed line. These water-dependent species seem to prefer wet places in dry areas.

curs from northern Colombia, Venezuela, and the Guianas S to Santa Fe and Corrientes, Argentina, and Paraná, but apparently with distributional gaps in the southern Guianas and adjacent Brazil, and in southern Amazonia to Maranhão. It is found in all but the southwestern chaco (Santiago del Estero-Tucumán area), but only in marshy locations. The chaco is at the southern extent of the species' range.

Pyrocephalus rubinus
Vermilion Flycatcher

Taxonomy. Polytypic species, monotypic genus.

Ecology. In woodland edge, savanna, pampas, and desert; territorial, nests in bushes. Partly migratory.

Distribution and variation. New World, from Nearctic to southern South America. Within South America it occurs disjunctly in northern Colombia, Venezuela, and Guyana, in western Ecuador to northern Chile, in southeastern Peru, and in southern Bolivia and western Paraguay S to Neuquén, Río Negro, and Uruguay. The migratory, southern disjunct population, *P. r. rubinus*, has a small bill, and is less bright red than other races. It breeds in all the chaco except Mato Grosso, northern Paraguay, and Santa Cruz, Bolivia, and extends beyond the chaco to the E (eastern Paraguay, Rio Grande do Sul, Uruguay), the S (Buenos Aires, Río Negro), and the W (monte and open areas in dry subtropical forest from southern Bolivia to Mendoza). Its northern breeding limits are uncertain, and it may breed throughout the chaco.

Satrapa icterophrys
Yellow-browed Tyrant

Taxonomy. Monotypic genus and species.

Ecology. A forest edge, woodland, and brushland species, nesting in a cup nest in a tree or bush, even in orchards or eucalypts. Territorial. Partly migratory.

Distribution. Endemic in central South America from northern Bolivia, central Mato Grosso, and Maranhão S throughout Brazil, Paraguay, and Uruguay to Tucumán, Córdoba, and northern Buenos Aires. It occurs throughout the chaco and beyond it somewhat to the S and W, and farther to the E and N.

Machetornis rixosus
Cattle Tyrant

Taxonomy. Polytypic species, monotypic genus, of uncertain relatives.

Ecology. This is a ground-foraging tyrant that seeks insects as it walks about, often springing upward after departing prey. Territorial, partly migratory.

Distribution and variation. Endemic in South America. Two races comprise a disjunct northern group of populations in northern and northeastern Colombia and the savanna region of Venezuela. *Machetornis rixosus rixosus*, the thinner-

billed, smaller, and less rufous (wings, tail) southern disjunct race, occurs from central-northern Bolivia, northern Mato Grosso and Maranhão throughout eastern and southern Brazil, Paraguay, and Uruguay to Tucumán, Córdoba, and Buenos Aires. This race occurs in open parts of the entire chaco region, and beyond it to the W (cultivated and pastured areas in Andean foothills), S (pampas), E (to the Atlantic Coast), and N.

Tyrannus savanna
Fork-tailed Flycatcher

Taxonomy. Polytypic. Merged into *Tyrannus* by Smith (1966), and formerly called *Muscivora tyrannus*.

Ecology. Found in savanna and open country, migrating in groups, but territorial when nesting. Highly migratory.

Distribution and variation. Middle and South America. In South America it occurs in northern Colombia, and eastern Colombia E to Guyana, and, disjunctly, from the lower Amazon River and Maranhão S through central Brazil, eastern Bolivia, and Paraguay to western São Paulo, Rio Grande do Sul, Uruguay, and Río Negro, Argentina. Weakly differentiated races are distinguished on the basis of the shape of outer primaries in males, and minor color variation. The race *savanna* occurs throughout the disjunct southern range of the species except for the lower Amazon region. It breeds throughout the chaco in open places and woodland edges, and it extends beyond the chaco in all directions (slightly to W, extensively in other directions).

Tyrannus melancholicus
Tropical Kingbird

Taxonomy. Polytypic. Forms a superspecies with *T. couchii* of Middle America to southern Texas (see Mayr and Short, 1970).

Ecology. Frequents forest clearings and edges, savannas, open country about habitations, and riparian situations in deserts. Migratory. Territorial. Nests in trees.

Distribution and variation. New World from Nearctic to Patagonia. In South America, *melancholicus* occurs S to central Peru W of the Andes,

and it is found throughout the eastern lowlands S to Río Negro, Argentina. *Tyrannus melancholicus melancholicus* is slightly larger than northern and eastern races and has a grayer throat and broader greenish chest band, but variation is considerable. This form occurs throughout Amazonia from southern Venezuela S (southeastern Colombia, eastern Ecuador, eastern Peru, western Brazil) through northern Bolivia, and from there E to Bahía and Espíritu Santo, and S through Brazil, Paraguay, Uruguay, and Argentina to Río Negro. It is found throughout the chaco, and beyond it in all directions.

Empidonomus varius
Variegated Flycatcher

Taxonomy. Polytypic. No very close congeneric relatives.

Ecology. A woodland and forest flycatcher. Migratory.

Distribution and variation. Endemic in South America, from Venezuela, the Guianas, and eastern Colombia S throughout the lowlands, including all of Brazil, to Paraguay, northwestern Uruguay, and San Luis, La Pampa, and Buenos Aires, Argentina. The southern of the two races, *varius*, is larger and has more discrete ventral streaking than the northern form. *Empidonomus varius varius* occurs from eastern Bolivia, northern Mato Grosso, Minas Gerais, and Espírito Santo S through the southern portion of the species' range. It is found in all parts of the chaco, W of it in the dry subtropical forest, and to the N, E, and S (southward mainly in chaco scrub).

Empidonomus aurantioatrocristatus
Crowned Slaty-Flycatcher

Taxonomy. Polytypic. This species has no very close relatives.

Ecology. A brushland and edge species, found particularly along streams in open country, and in woodlands and savannas. Migratory. Territorial.

Distribution and variation. Endemic in South America. It occupies northeastern Brazil from the lower Amazon to Piauí and southern Pará, and disjunctly, in the chaco and pampas from

Paraguay and southern Bolivia to Mendoza, La Pampa, Buenos Aires, and Uruguay. The southern population is racially distinct (*aurantioatrocristatus*); it is larger, and darker gray than the northern form. It inhabits the chaco except for Santa Cruz, Bolivia, and Mato Grosso and extends beyond the chaco W into dry subtropical forest and monte, S through most of the pampas to La Pampa, and E to Misiones, Rio Grande do Sul, and Uruguay.

Legatus leucophaius
Piratic Flycatcher

Taxonomy. Polytypic species, monotypic genus.

Ecology. Forest, woodland, and savanna flycatcher, territorial, and probably partly migratory, as it is in Central America.

Distribution. New World, Mexico to Argentina. Found in South America from northwestern Ecuador and northern Colombia E and S through the lowlands to Tucumán, Chaco, and Corrientes, Argentina, and Rio Grande do Sul. *Legatus l. leucophaius* occurs from Nicaragua to Argentina. Within the chaco it is found in all but the southeastern edge of the chaco in Santa Fe, and the central Argentine chaco. From the chaco it extends N, E, and slightly to the W.

Megarhynchus pitangua
Boat-billed Flycatcher

Taxonomy. Polytypic species, monotypic genus.

Ecology. Large forest and forest-edge species also found in riverine woods of savannas. Territorial. Nonmigratory. Preys on insects, small lizards, small fish.

Distribution and variation. New World, Mexico to Argentina. In South America it occurs S to northwestern Peru, northern Colombia, and in the E throughout the lowlands S to Paraguay, eastern Formosa, Corrientes, and Paraná. *Megarhynchus pitangua pitangua* is the race inhabiting eastern South America from northern Colombia E and S. It is large in size, with a very green back, and its bill is the widest and deepest of all the races. This form is found in most of the eastern chaco (probably S to Chaco Province), and the

northern chaco (virtually all of the Paraguayan chaco, and the Bolivian and Mato Grosso chaco). It extends N and NE from the chaco.

Myiodynastes maculatus
Streaked Flycatcher

Taxonomy. Polytypic. Very closely related to the partly sympatric *M. luteiventris* of the United States to Costa Rica, from which it differs mainly in its larger bill, paler color below, and paler chin.

Ecology. Found in treetops in diverse partly open forests and woodlands and forest edges, including scattered trees in savannas and pampas. Migratory.

Distribution and variation. Middle and South America. It is found S to northwestern Peru and central Argentina in South America. In the E it occurs throughout the lowlands and lower Andean slopes to La Rioja, La Pampa, Buenos Aires, and Uruguay. *Myiodynastes maculatus maculatus*, a large, dark, dorsally less rufous, and ventrally more heavily streaked subspecies, inhabits southern Brazil S from southwestern Amazonia to Maranhão, eastern Peru, northern and eastern Bolivia, Paraguay, Uruguay, and northern Argentina as indicated in the species' range. It occupies the entire chaco, and extends beyond it in all directions.

Pitangus sulphuratus
Great Kiskadee

Taxonomy. Polytypic. Related to the sympatric *P. lictor*.

Ecology. Large forest, savanna, and open country flycatcher, foraging on insects and small lizards. Territorial. Partly migratory.

Distribution and variation. New World from Texas to central Argentina. In South America from northern Colombia through the eastern lowlands and Andean slopes to Mendoza, San Juan, La Pampa, Buenos Aires, and Uruguay. The southern race *bolivianus* is larger and less rufous than other forms. It is found from south-central Bolivia, Paraguay, Misiones, and Rio Grande do Sul southward. This form ranges throughout the chaco, which forms its northwestern boundary; it

ranges slightly W and more extensively SE and S from the chaco.

Myiarchus ferox

Short-crested Flycatcher

Taxonomy. Polytypic. Relationships in this genus currently are under study by Lanyon.

Ecology. Forest, woodland, and savanna flycatcher, nesting in crevices or holes in trees. Territorial. Nonmigratory.

Distribution and variation. Southern Middle America to northern Argentina and Uruguay. In South America it inhabits lowlands and lower slopes from northern Colombia throughout countries S to Tucumán, and Córdoba in western Argentina, and farther E, to Uruguay, Misiones and parts of Corrientes. The southern race *australis*, a pale (especially crown) form, is found S from northern Bolivia, Mato Grosso and Rio de Janeiro. It ranges through all of the chaco, and slightly to the S and W, and more extensively to the N. In the E it is sporadic across Corrientes and of uncertain status in eastern Paraguay.

Myiarchus tyrannulus

Brown-crested Flycatcher

Taxonomy. Polytypic. Forms a superspecies with *M. crinitus* of the Nearctic (Mayr and Short, 1970).

Ecology. Chiefly of forest-edge, woodland, and shrub desert, nesting in cavities in trees or cacti. Migratory.

Distribution and variation. Widespread in New World, United States of America to Argentina. In South America it occurs (widely disjunct from Middle American populations) in northeastern Colombia, northern Venezuela, and the Guianas through the lower Amazon Valley, throughout eastern Brazil and W through Mato Grosso to northern Bolivia and eastern Peru (possibly lacking in central Amazonia); it ranges S to La Rioja, Córdoba, western Corrientes, eastern Paraguay, and Paraná. *Myiarchus tyrannulus tyrannulus*, one of many races, is weakly differentiated (large, pale, with much rufous in tail); it occurs from eastern Peru and adjacent Brazil S through northern and eastern Bolivia and Paraguay to the Argentine chaco and slightly beyond it (into La Rioja, Córdoba, Corrientes). It

ranges E to central Mato Grosso. This form is found in all parts of the chaco, in the dry subtropical forest to the W, somewhat E and N of the chaco, and far to the NW. Its northern limits in central Brazil are uncertain.

Myiarchus swainsoni

Swainson's Flycatcher

Taxonomy. Polytypic. Its relationships are yet to be determined within *Myiarchus*.

Ecology. Inhabits forest, woodland, and brushland. Territorial and hole-nesting. Migratory.

Distribution and variation. Endemic in South America. Found from the southern edge of Venezuela, Guyana and Surinam SW through Amazonia, including southeastern Brazil and northern Bolivia; eastward S of the Amazon to its mouth and S through all of southern Brazil, eastern Bolivia, and Paraguay, to La Rioja and Buenos Aires, Argentina, and northern Uruguay. The southeastern Brazilian (and adjacent Paraguay, northeastern Argentina, and northern Uruguay) *M. s. swainsoni* is strongly differentiated from other races (i.e., the *pelzelni* group) by virtue of its very dark coloration both dorsally and ventrally. It intergrades with *M. p. pelzelni* and *M. p. ferocior*. The latter race, distinguished from more northern *pelzelni* by its larger size, occurs throughout the chaco and beyond it to central eastern Bolivia, the dry subtropical forest from Bolivia to Tucumán, monte SW to La Rioja, and chaco scrub S to La Pampa and Buenos Aires. This race intergrades (actually hybridizes; *ferocior* is distinct morphologically and vocally from *swainsoni*) with *swainsoni* from southern Mato Grosso through central Paraguay to western Corrientes, including the pantanal region of the entire eastern chaco (Lanyon, in prep.).

Contopus cinereus

Tropical Wood Pewee

Figure 47

Taxonomy. Polytypic. I consider this pewee very closely related to the hybridizing, northern (Nearctic, Central American) *C. virens* and *C. sordidulus*, and the three here are placed in a single superspecies (see Mayr and Short, 1970). *Contopus sordidulus* often is merged in *C. virens*.

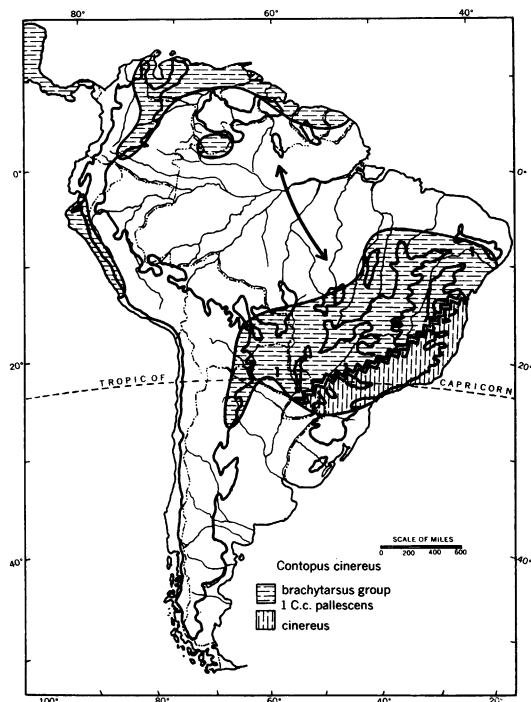


FIG. 47. Range of Tropical Wood Pewee (*Contopus cinereus*). Isolates of *brachytarsus* subspecies group are indicated, and include (see arrow) *pallescens* in the southeastern region, where it interbreeds with well-differentiated *C. c. cinereus* in apparent secondary contact. Distribution is in lowland savanna, woodland and forest edges, with wet forest gaps.

Contopus cinereus resembles these northern species in coloration, generally small size (compared with the *fumigatus* group), and its narrow, short, weakly flattened bill (compared with West Indian pewees, the “*Blacicus*” group). It differs from *sordidulus* and *virens* in its smaller size, shorter wings (the northern species are highly migratory, *cinereus* is nonmigratory except possibly for extreme southern populations—see Olrog, 1963), and generally darker crown.

Ecology. Forest and forest edge species, flycatching for food at all levels in trees. May be migratory (see above). Territorial.

Distribution and variation. Discontinuously distributed in Middle and South America. It is found in western Ecuador and northwestern Peru, in central and northeastern Colombia,

across northern Venezuela and the Guianas, in southernmost Venezuela, and in central South America from Maranhão, Piauí, and Pernambuco SW through Mato Grosso to eastern Bolivia, and S to Tucumán in western Argentina, central Paraguay, Misiones, and Paraná. *Contopus cinereus pallescens* occurs from Tucumán N to central Bolivia and E across Paraguay and eastern Bolivia, most of Mato Grosso, Goiás, Minas Gerais, and Bahía to Pernambuco and Maranhão. This form is brown capped, and pale generally with a pale gray breast and yellowish belly. It closely resembles, and indeed seems a representative of, the northern *brachytarsus* group. It meets the strongly differentiated (black-capped, very dark above, grayish ventrally) *C. c. cinereus* of southeastern Brazil (and Misiones) along a line from eastern Paraguay through São Paulo and Minas Gerais to southern Bahía. *Contopus cinereus pallescens* may be a recent (secondary) invader from the N. This last-mentioned subspecies inhabits the northern chaco (Paraguayan chaco, Santa Cruz, Mato Grosso) and perhaps the fringes of the western chaco in Salta.

Empidonax euleri Euler's Flycatcher

Taxonomy. Polytypic. I assign *euleri*, Middle American *albigularis*, and western Ecuadorian-northwestern Peruvian *griseipectus* to the same superspecies. These are very similar in appearance, and allopatric. *Empidonax albigularis* resembles *euleri* but has the white throat more discrete in a definite patch. It is less olive below, but dorsally matches *euleri*, even having browner and greener races as *euleri* does; they have a similar bill. *Empidonax griseipectus* is similar in size and bill shape to *euleri*; it seems like a “washed out” version of *euleri*, with a grayer tone, and it is less greenish (this varies greatly, however). Its wing bars are white instead of brownish.

Ecology. Small forest, woodland, and brushland flycatcher, often found near water. Migratory.

Distribution and variation. Endemic in eastern South America. Found from eastern Colombia and northern Venezuela SW through the llanos to Amazonia (eastern Ecuador, eastern Peru, northern Bolivia, western Brazil) and east-

ward S of the Amazon to its mouth (although its status is uncertain in parts of the region S of the Amazon River), and to the eastern corner of Brazil, although questionably in northern Maranhão, and S through eastern Bolivia, all of south-central and southern Brazil, and Paraguay to Uruguay, northern Buenos Aires, Santa Fe, Tucumán, and possibly La Rioja, Argentina. An apparently disjunct population inhabits the Guianan highlands. The northern green-backed (*lawrencei* group) populations are distinct from the southern brown-backed (*euleri* group) populations of eastern Bolivia, Mato Grosso, and southern Bahía southward. The latter group consists of a slightly larger, browner, ventrally paler, dorsally less rufescent western race, *argentinus*, and eastern *E. e. euleri*. The race *argentinus* occurs from eastern Bolivia, western Paraguay, and Tucumán, E to central Mato Grosso, eastern Paraguay, and the Uruguay River, in which area it intergrades with *euleri*. Thus, *argentinus* inhabits the entire chaco, and extends beyond it somewhat in all directions.

Cnemotriccus fuscatus
Fuscous Flycatcher

Taxonomy. Polytypic species, monotypic genus.

Ecology. Forest and forest-edge flycatcher frequenting lower strata of trees. Nonmigratory. Territorial.

Distribution and variation. Endemic in South America. Occurs in northern and central Colombia, in northern Venezuela, and in southernmost Venezuela, the Guianas, southeastern Colombia, eastern Peru and northern Brazil S through Amazonia (but not central-eastern Brazil) to northern and eastern Bolivia, Mato Grosso, and E to Pernambuco, and S to eastern Paraguay, northern Santa Fe, and Rio Grande do Sul. Of the several races, the widespread, well-marked *bimaculatus* is found in the chaco of Santa Cruz, Bolivia, the pantanal of Mato Grosso and northernmost Paraguay, the northeastern Paraguayan chaco (Fort Wheeler), and in Santa Fe and probably Chaco Province. It extends E from the chaco to western Rio Grande do Sul, western Paraná, western São Paulo, and western Bahía, NE to Goiás, N to Pará

and Maranhão (which it reaches from the W), and NW to southeastern Peru. This form is large, it lacks the olive tone of other races, it is generally pale (especially on the underparts), and its rump is very rufous.

Myiophobus fasciatus
Bran-colored Flycatcher

Taxonomy. Polytypic. It forms a superspecies with northeastern Peruvian *cryptoxanthus*, which has been merged in *fasciatus* by some authors. *Myiophobus cryptoxanthus* is streaked ventrally, although less so than *fasciatus*. It is less brown and greener dorsally, yellower on the abdomen, and its bill is a trifle shorter and broader than that of *fasciatus*, which it otherwise resembles.

Ecology. This small flycatcher forages in the edges of forests, partly cut-over woodlands, savannas, brushland, and shrub desert. Possibly migratory.

Distribution and variation. Southern Middle America and South America. It is found disjunctly in northern Colombia to northern Chile in the W, from northeastern Colombia to French Guiana in northern South America, and from southeastern Peru, northern Bolivia, Mato Grosso, Pará (Amazon Delta), and Maranhão S throughout southern Brazil (except extreme northeastern corner), eastern Bolivia, Paraguay, and Uruguay, to Catamarca, Córdoba, and northern Buenos Aires. Of the many races, *auriceps* (combines a rust-tone dorsally with pale brown ventral streaks on a very white background) frequents the chaco generally, and extends beyond it slightly to the S and the W, and extensively to the NW (northern Bolivia, southeastern Peru).

Hirundinea ferruginea
Swallow Flycatcher

Taxonomy. Monotypic genus, polytypic species.

Ecology. Frequents forests, especially about steep-sided banks of streams, woodland, and savannas. Peculiar swallow-like flight. Nonmigratory.

Distribution and variation. Endemic in South America, ringing the Amazon, in the N from the

Guianas, southern Venezuela, and adjacent northern Brazil to eastern Colombia and eastern and central Peru, and in the S from eastern Pará, Maranhão, and Rio Grande do Norte S throughout eastern Brazil to Uruguay, and W through Goiás and Mato Grosso to Paraguay, northern and eastern Bolivia and western Argentina S to La Rioja and Córdoba (E to Chaco and Formosa provinces). The southern *bellicosa* group has been considered specifically distinct from northern *ferruginea*. It is much paler brown and more rufous above with a rufous (not brown) rump, a mainly rufous, dark-tipped tail (versus brown tail, or with some rufous basally), and a shorter, narrower bill than *ferruginea*. Western *H. f. pallador* of the *bellicosa* group is paler rufous above and below than *bellicosa*. The subspecies *pallador* occurs in all but the southeasternmost corner of the chaco; it extends beyond the chaco to the SW (Córdoba, La Rioja), the W (dry subtropical forest, monte), the NW (to northern Bolivia), and the N (northern Santa Cruz, Bolivia). It meets *bellicosa* along the Paraguay River of Paraguay and in the pantanal of Mato Grosso.

Tolmomyias sulphurescens
Yellow-olive Flycatcher

Taxonomy. Polytypic. Closely related to sympatric *assimilis*.

Ecology. Small, inhabits forest and woodland. Nonmigratory. Territorial. Hanging nest with a side entrance (Haverschmidt, 1968).

Distribution and variation. Middle and South America. It occurs from northwestern Peru N to Colombia, and from northeastern Colombia, Venezuela, and the Guianas S throughout Brazil, and lowlands of the countries extending E of the Andes to northern and eastern Bolivia, western Argentina to Tucumán, central and eastern Paraguay, and eastern Argentina to Santa Fe and Corrientes. One, and probably two races occur in the chaco. Eastern *grisescens*, a pale, dull grayish form, occupies the eastern chaco and pantanal from northern Paraguay and Mato Grosso to northern Santa Fe, and E to eastern Paraguay. *Tolmomyias sulphurescens pallescens*, with pale wing margins, pale coloration generally, and very light green ventral color, occurs from Mato Grosso and northern Bolivia to the pantanal of

Mato Grosso and southern Santa Cruz (where it presumably intergrades with *grisescens*) and the dry subtropical forest S to Tucumán. This subspecies occupies the Santa Cruz and Mato Grosso chaco, and it may reach the western chaco fringes in Argentina. It is unlikely that either race inhabits the xeric central chaco region.

Todirostrum margaritaceiventer
Pearly-vented Tody-tyrant

Taxonomy. Polytypic. I follow Meyer de Schauensee (1966) in considering *impiger*, *septentrionalis*, and *duidae* conspecific with *margaritaceiventer*. Of these, *duidae* is the most distinct (it is very large, ochraceous below, with ventral streaks obscure, and it is very dark cinereous dorsally; possibly it is specifically distinct). I find no clear-cut difference between *Idioptilon* and *Todirostrum*, and so merge them (see Meyer de Schauensee, 1970). This species is sympatric with other close relatives.

Ecology. Long, flat-billed flycatcher of shrubbery in woods, at woodland edges, and in savannas. Nonmigratory.

Distribution and variation. Endemic in South America discontinuously, in the Magdalena Valley region of Colombia and northern Colombia, in northern Venezuela, in southern Venezuela, in central and southern Peru, and from northern Bolivia, Mato Grosso, Maranhão, and Pernambuco through interior eastern Brazil (western Bahía, western Minas Gerais) to Paraguay and northern Argentina S to Tucumán, Córdoba, and Entre Ríos. From eastern Bolivia, Mato Grosso, and Goiás S through Paraguay to Argentina occurs *T. m. margaritaceiventer*, a contrastingly colored (less green; grayer above, with especially gray head, intermediate back, and green rump) race. This form is found throughout the chaco, barely beyond it to the S (Córdoba), somewhat beyond it to the E (to Uruguay River) and W (lower Andean slopes), and extensively beyond it to the limits of the subspecies' range in the N, NW, and NE.

Euscarthmus meloryphus
Tawny-crowned Pygmy-tyrant

Taxonomy. Polytypic. Genus monotypic.

Ecology. Very small forest edge, brushland, and savanna flycatcher. Nonmigratory.

Distribution and variation. Endemic in South America. Populations occur in northern Colombia and northern Venezuela, in western Ecuador and northwestern Peru, in northern Bolivia, central Mato Grosso, Maranhão, and Ceará S to Tucumán in the W, southern Mato Grosso, easternmost Paraguay, Misiones, and Paraná, and apparently disjunctly in eastern Formosa and eastern Chaco, in Córdoba, in Entre Ríos, and in western Uruguay. The widespread, southern *meloryphus* includes all the main southern populations, except those in eastern Bahía, Ceará, and Pernambuco, and it also includes the southern small isolated populations. This form has a well-defined cap, and is brown-green above. Variation is clinal from large, gray birds in the SW, to smaller and greener birds in the NE (and then to small, gray *fulvicepsoides* in the far NE). This race inhabits the chaco of eastern Chaco Province, eastern Formosa, possibly the eastern Paraguayan chaco, and the fringes of the chaco in Santa Cruz, Bolivia, and in the western Argentine chaco.

Pseudocolopteryx dinellianus
Dinelli's Doradito and
? *Pseudocolopteryx acutipennis*
Subtropical Doradito

Taxonomy. Both monotypic. These species are similar in size and bill shape, and both thus differ from the related, thin-billed *flaviventris*; they also tend to be greener, with a green rump, lack strong rufous coloring and streaking, and have narrowed inner primaries like the otherwise quite different *P. sclateri* (primaries normal in *flaviventris*). *Pseudocolopteryx dinellianus* is pale brown-green above, with brown in the crown (and a trace of rufous), whereas *acutipennis* is green throughout the upper parts. They overlap in Tucumán.

Ecology. Both frequent brushland and shrubbery, *dinellianus* in the xeric chaco, and *acutipennis* in the dry subtropical forest. *Pseudocolopteryx acutipennis* is migratory (along the Andes and also to Paraguay; specimens in AMNH), as is *P. dinellianus* (to Bolivia, Paraguay).

Distribution. The superspecies is endemic in south-central South America. *Pseudocolopteryx dinellianus* occurs in the southern chaco from Santa Fe to Tucumán, and possibly breeds northward in the central chaco to Paraguay, although Paraguayan specimens appear to be migrants. *Pseudocolopteryx acutipennis* breeds along the Andes from La Rioja N at least to central Bolivia, and possibly farther. This species may breed in the western fringes of the Paraguayan and Argentine chaco.

Pseudocolopteryx sclateri
Crested Doradito

Taxonomy. Monotypic. Related to *acutipennis* and *dinellianus*.

Ecology. Small flycatcher of low shrubbery near water. Migratory.

Distribution. Endemic in South America (and Trinidad). It has a disjunct distribution, breeding in Trinidad and probably in Guyana, and in southern Brazil from Mato Grosso, São Paulo, and Paraná S through central and eastern Paraguay to the entire Parana-Paraguay river area of Argentina (as far as Buenos Aires), and Rio Grande do Sul. Its northern breeding limits are uncertain; it migrates as far as Bahía. It occurs in the chaco primarily in the pantanal region from Mato Grosso to Santa Fe, but also in the eastern chaco woodland to some extent. Its range extends mainly E from the chaco, but also S along the Parana River.

Pseudocolopteryx flaviventris
Warbling Doradito

Taxonomy. Monotypic. See *P. dinellianus* above.

Ecology. Shrub and brushland flycatcher, but in open country, not forests. Migratory in part.

Distribution. Endemic in southern South America, disjunctly in central Chile, and in Argentina from Chubut N throughout the pampas and chaco scrub to Tucumán, the pantanal region to Corrientes and Santa Fe, and probably to northern Paraguay and Mato Grosso, and to Rio Grande do Sul and Uruguay. It occurs in the southeastern edge of the chaco and probably throughout the pantanal; the chaco forms its northern limit of breeding.

Polystictus pectoralis
Bearded Tachurí
Figure 48

Taxonomy. Polytypic. Forms a superspecies with *P. superciliaris* of Minas Gerais and Bahía. The latter has a similar bill, but is gray (versus pale rusty brown) above, with a gray instead of brown cap and fawn and white (versus tawny and yellow-white) underparts.

Ecology. A bird of bushy open country, including savannas, pampas, woodland edges, and scrub desert, especially near water. Nonmigratory.

Distribution and variation. The superspecies is endemic in South America. *Polystictus pectoralis* occurs in two widely separated areas, central Colombia and central Venezuela to Guyana (two races), and from eastern Bolivia, central Mato

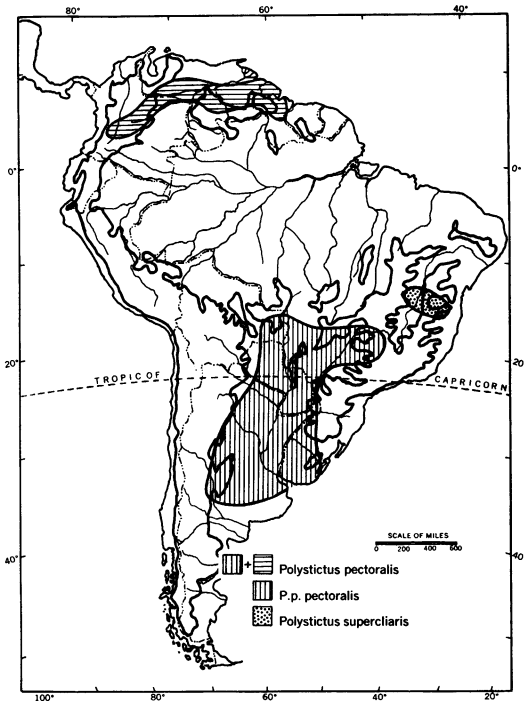


FIG. 48. Range of Bearded Tachuri (*Polystictus pectoralis*) and its allospecies *P. superciliaris*. Former has racial isolates in north and south; latter is isolated in caatinga region. Distribution of *pectoralis* is llanos-chaco-pampas-chaco scrub, entering campo and some forests.

Grosso, and western São Paulo S through Paraguay to western Rio Grande do Sul, Uruguay, Buenos Aires, La Pampa, and Mendoza (*P. p. pectoralis*). The latter form is larger than the northern races, and less rufous than one of them (*bogotensis*). It occurs throughout the eastern and central chaco and from there to the E and S. Within the chaco it is found in the pantanal and the more open parts of the chaco woodlands.

Culicivora caudacuta
Sharp-tailed Tyrant

Taxonomy. Monotypic genus and species.

Ecology. Small flycatcher of brushy edges of forests and brushy areas in savannas. Nonmigratory. Territorial.

Distribution. Endemic in central South America from eastern Bolivia and central Mato Grosso to western São Paulo and S through eastern Paraguay to Misiones, Corrientes, and northern Santa Fe. It inhabits the northeastern (Santa Cruz, Bolivia, and Mato Grosso) chaco and the southeastern chaco (eastern Chaco Province, northern Santa Fe), and occurs from there E and slightly N.

Stigmatura budytoides
Greater Wagtail-tyrant
Figure 49

Taxonomy. Polytypic. Forms a superspecies with *S. napensis*, the only other congeneric species (they may be conspecific), which occurs disjunctly in the upper and middle Amazon Valley (eastern Peru E to Rio Tapajós), and in Pernambuco and Bahía. Studies are needed of interactions between *budytoides* and *napensis* in Pernambuco and northern Bahía, where they seem to meet (see Meyer de Schauensee, 1966, p. 376). *Stigmatura budytoides gracilis*, which seems to meet *S. n. bahiae*, differs in its larger size, longer and heavier bill, grayer, less brown upperparts, and lack of a buffy ventral cast found in *bahiae*. *Stigmatura napensis napensis* more closely resembles *S. budytoides* than does *S. n. bahiae*, but its bill is narrower, it is smaller, and greener above than *budytoides*. The forms *bahiae* and *napensis* are considered conspecific chiefly because both show pale bases of the outer rectrices, a feature lacking in the four subspecies of *budytoides*.

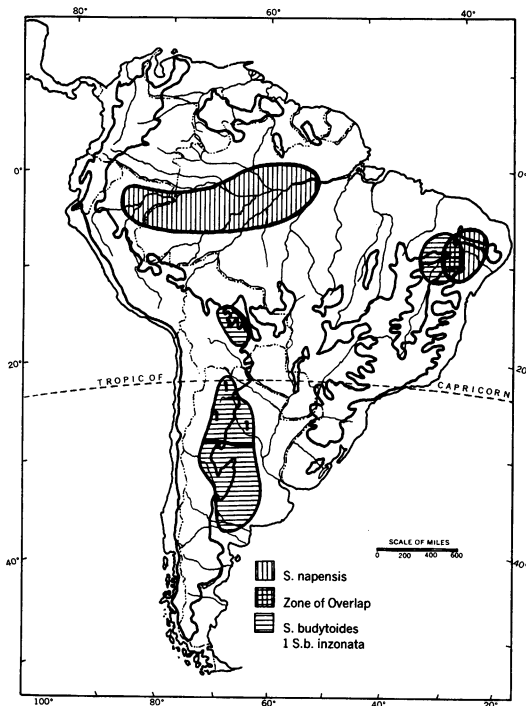


FIG. 49. Range of Greater Wagtail-Tyrant (*Stigmatura budytoides*) and its allospecies *S. napensis*. Three isolates of *budytoides* are shown. Interactions between two species in northeast are unknown; they meet and may or may not overlap as shown. Distribution of *budytoides*, chaco scrub and subandean "monte," plus caatinga, barely reaching southwestern chaco.

Ecology. Brushland flycatcher that cocks its tail, wrenlike. Migratory.

Distribution and variation. The superspecies is endemic in South America, *budytoides* occurring in three disjunct groups of populations: in Pernambuco, Bahía, and Piauí; in central Bolivia; and in Argentina from Salta and Santiago del Estero S through the monte and chaco scrub to Buenos Aires, Río Negro, and sporadically to Chubut. Inhabiting the southwestern chaco (Santiago del Estero) and from Salta to Catamarca, La Rioja, and Córdoba is *S. b. inzonata*, weakly distinguished from the more southern, contiguous *flavocinerea* by its clearer pale yellow underparts (less grayish olive); both differ from disjunct northern races in their pale ventral coloration. There is some question as to how far north

inzonata may breed (possibly to Paraguay; Paraguayan specimens seem to be migrants).

Serpophaga subcristata
White-crested Tyrannulet
Figure 50

Taxonomy. Polytypic. Includes "munda" as both a subspecies and a morph. This form is identical with *S. subcristata subcristata* except that it is whiter throughout (lacks yellow ventrally, in back, under wings). Both occur together in central Argentina (see Bó, 1969).

Ecology. Small flycatcher of dense shrubbery, either in forests or brushy areas of woodlands, pampas, and monte. Migratory.

Distribution and variation. Endemic in south-central South America from Piauí and Pernambuco S through southeastern Brazil to Paraná and

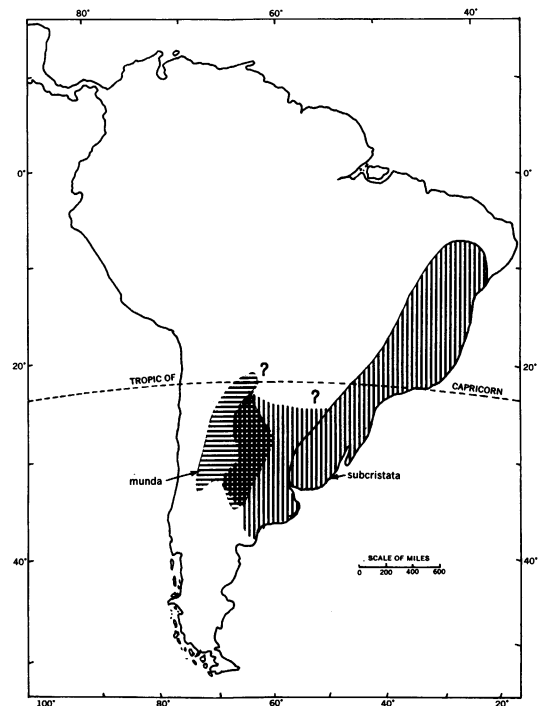


FIG. 50. Range of White-crested Tyrannulet (*Serpophaga subcristata*). Eastern and western forms overlap (crosshatching), behaving as morphs in overlap area. Distribution, southeastern Brazilian forest, caatinga, chaco scrub, chaco, pampas, and dry subtropical forest.

Rio Grande do Sul, and beyond to southeastern Paraguay, Uruguay, and Jujuy, Tucumán, Mendoza, La Pampa, and Río Negro, Argentina. It is questionable whether the species breeds north of Santiago del Estero and Chaco Province (migratory to Bolivia, most of Paraguay, Mato Grosso) in the W, and its status in the northern portion of its Brazilian range is uncertain. Variation is to some degree clinal, the eastern *stramineus* (Uruguay, southeastern Brazil) being very yellow below, and olive-backed, *subcristata* of eastern Argentina being paler yellow below and less olive above, and western *munda* being entirely white below and gray-backed. *Serpophaga subcristata subcristata* occurs from Misiones, the Corrientes-eastern Paraguay border region, Chaco Province, Santiago del Estero, and Tucumán S and E through Córdoba, Santa Fe, La Pampa, and Buenos Aires to Río Negro. *Serpophaga subcristata munda* breeds from Jujuy and Salta S in monte and dry subtropical forest edges to Mendoza, and to La Pampa; it occurs apparently as a morph of *subcristata* with the latter in Tucumán, Santiago del Estero, Santa Fe, Córdoba, and La Pampa. Thus, *subcristata* occurs across the southern chaco from Chaco Province to Tucumán, *munda* occurs with *subcristata* in most of that area (except extreme E), and *munda* may occur in "pure" form at the western edge of the chaco in Salta. The species extends beyond the chaco to the S (chaco scrub zone, pampas), the SW (monte zone), and to the E (pampas and forest).

Serpophaga nigricans
Sooty Tyrannulet

Taxonomy. Monotypic. This species seems very closely related to *S. hypoleuca* of northern Amazonia to eastern Pará, and in central Venezuela. Both have a narrower bill than does *S. cinerea* or even *S. subcristata*, and their tails are similar (neither short as in *cinerea*, nor long as in *subcristata*). The southern *nigricans* is larger than *hypoleuca*, it is more olive-gray and less brown-gray above, its crown lacks black around the white patch, and it is cinereous gray below rather than pale grayish white as in *hypoleuca*. *Serpophaga nigricans* and *S. hypoleuca* are treated here as allospecies of a single superspecies.

Ecology. Brushland flycatcher of the chaco, dry subtropical forest, and chaco scrub. Migratory.

Distribution. The superspecies is endemic in South America. *Serpophaga nigricans* breeds from southern Bolivia and adjacent western Paraguay S through the dry subtropical forest, monte, and central and western chaco to Mendoza, Neuquén, and Río Negro. Possibly it breeds in northeastern Argentina, and farther N in Paraguay than indicated above. It seems not to breed in the pantanal and adjacent chaco woodlands, but it is found throughout the central and western chaco N at least to the southwestern Paraguayan chaco. Its range extends mainly S from the chaco.

Inezia inornata
Plain Tyrannulet

Taxonomy. Monotypic. This species seems to form a superspecies with *I. tenuirostris* of northeastern Colombia and northwestern Venezuela. Both have narrower bills than *I. subflava*. *Inezia inornata* is larger and longer-billed than *tenuirostris*, it is gray-green above instead of brownish yellow-green, and it is gray and whitish yellow, not pale yellow, below. Further study is needed to fully establish their relationship.

Ecology. A woodland and savanna shrub species found in the chaco, campos, and forest edge. Nonmigratory.

Distribution. The superspecies is endemic in South America. *Inezia inornata* is found from northern Bolivia to west-central Mato Grosso, and S through western Paraguay to the fringe of Argentina in Salta. It occurs in the northern chaco from Salta through northwestern Paraguay to the Bolivian and Mato Grosso chaco, thence NW, N, and NE.

Elaenia flavogaster
Yellow-bellied Elaenia

Taxonomy. Polytypic. Middle and South American *flavogaster* seems to represent West Indian *E. martinica* on the continent, and I consider them to form a superspecies. *Elaenia martinica* has the same bill shape as *flavogaster*; it is slightly larger and perhaps grayer throated. These species are closely related to *E. spectabilis*; the

latter is sympatric with *flavogaster* in eastern Paraguay, northeastern Argentina, and adjacent Brazil.

Ecology. *Elaenia flavogaster* is a forest, and forest edge flycatcher occurring in woodlands of savannas as well. Probably partly migratory.

Distribution and variation. Middle and South America. In South America S to northern Peru in the W, and in the E from northern Colombia, Venezuela, and the Guianas S through the eastern Amazon region to southeastern Peru, northern and eastern Bolivia, eastern Paraguay, Santa Fe and Corrientes, Argentina, and São Paulo. An isolated population occurs also in Tucumán, Argentina, and another is found in Cuzco, Peru. The area from southwestern and northern Colombia E and S through eastern South America is occupied by *E. f. flavogaster*, which occupies the eastern chaco, mainly in the pantanal throughout its extent (from Santa Cruz to Santa Fe; it is not common in this region). It extends E and N from there. It is possible that *flavogaster* occurs in the southwestern chaco in the vicinity of Tucumán. *Elaenia flavogaster flavogaster* is pale yellow below, and browner and less green above than races in Middle America and western South America.

Elaenia spectabilis

Large Elaenia

Taxonomy. Polytypic. Fairly closely related to *E. martinica* and *E. flavogaster* (see above).

Ecology. Forest and woodland elaenia. Territorial. Migratory.

Distribution and variation. Endemic in South America. Breeds from Tucumán N to central Bolivia in the W, and from Corrientes and Santa Fe N to central Paraguay and eastern Bolivia; E to Rio Grande do Sul and the Atlantic Coast N to São Paulo, and N to central Mato Grosso. Its status in eastern Brazil N of São Paulo is uncertain, but a distinct race (*ridleyana*) occurs on Fernando de Noronha Island off northeastern Brazil. The southern range (other than Fernando de Noronha) is occupied by *E. s. spectabilis* (more greenish, thicker billed than *ridleyana*). It occurs in the western edge of the chaco N from Tucumán to Paraguay, and in the eastern chaco from Santa Cruz and Mato Grosso to Santa Fe

and Corrientes. It extends slightly N and W, and extensively E, of the chaco.

Elaenia parvirostris

Small-billed Elaenia

Taxonomy. Monotypic. Forms a superspecies with *E. albiceps*, with which it is sometimes merged. The two species have similar bills and body proportions. *Elaenia parvirostris* is fully greenish (no brown) above, it has a paler throat and is smaller than *albiceps*, which is browner above, and darker and more greenish below, with a longer bill. *Elaenia albiceps* is a temperate zone species of the Andes from Colombia S, including all Andean countries; it breeds in lowland Argentina N to Buenos Aires.

Ecology. An abundant flycatcher of woodlands, woodland edges, and pantanal. Migratory. Forages at all levels, including low bushes.

Distribution. The superspecies is endemic in South America. Breeds from eastern Bolivia and southwestern Mato Grosso S to Catamarca and Tucumán, Argentina, in the W, and to Santa Fe, Uruguay, and Rio Grande do Sul in the E. It probably meets *E. albiceps* in the dry subtropical forest along the Andes. *Elaenia parvirostris* occurs in the western, northern, and eastern chaco (all but central Argentine chaco), and it extends beyond the chaco slightly to the W and NE (to eastern Paraguay), and more extensively to the SE.

Elaenia mesoleuca

Olivaceous Elaenia

Figure 51

Taxonomy. Monotypic. Forms a superspecies with the generally similar, but smaller-billed, grayer *E. strepera*, a dry subtropical forest elaenia of southern Bolivia to Tucumán.

Ecology. A forest elaenia, found in riparian woods in the Paraguay region. Forages in trees. Nonmigratory.

Distribution. The superspecies is endemic in south-central South America. *Elaenia mesoleuca* is found from Goiás and Bahía S through southeastern Brazil to Rio Grande do Sul and W to central Paraguay, eastern Formosa, and Santa Fe, Argentina. This species occurs in the southern part of the eastern chaco from central Paraguay

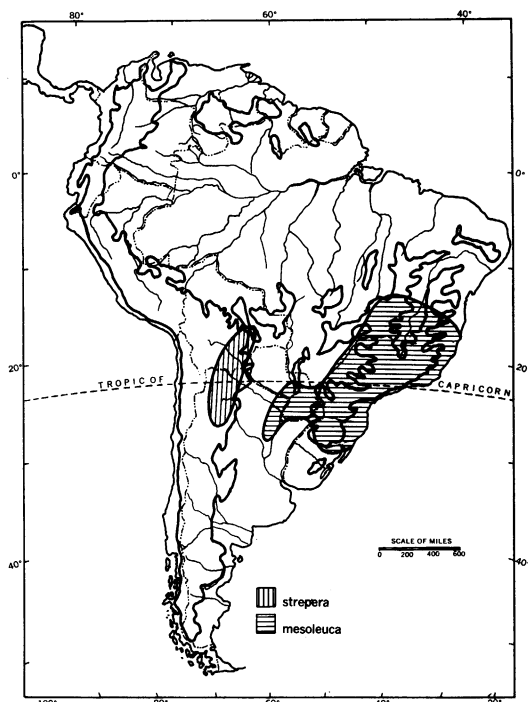


FIG. 51. Range of Olivaceous Elaenia (*Elaenia mesoleuca*) and its allospecies *E. strepera*. The two are isolated by dry central and western chaco. Distribution of *strepera*, forested southeastern Brazilian, but to surrounding ecological areas and wet chaco.

S, mainly along the Paraguay-Parana rivers and major tributaries, and from there E across eastern Paraguay and northern Corrientes to southeastern Brazil.

Suiriri suiriri
Suiriri Flycatcher
Figure 52

Taxonomy. Monotypic. I consider *S. affinis* of the lower Amazon River and Piauí S to Mato Grosso and Paraná to form a superspecies with *S. suiriri*; these are usually merged in a single species. I have failed to locate specimens showing intergradation of these two species, alluded to by Meyer de Schauensee (1966, p. 384, from a J. T. Zimmer MS). As their ranges approach each other very closely (northeastern Paraguay, western Mato Grosso), and there is no sign of intergrada-

tion, it seems best to treat them as species, especially because they differ rather markedly for flycatchers. *Suiriri suiriri* is smaller, grayer, with a much shorter bill, a black tail with less white tips and no white at the bases, a dark rump, and (usually) no yellow below; *S. affinis* is larger, yellow below, with a pale rump, a white-based, pale tipped tail, and a longer, heavier bill.

Ecology. Abundant flycatcher of brushy areas, forest edges, and bushes in open country (pampas). Territorial. Migratory.

Distribution. The superspecies is endemic in South America. *Suiriri suiriri* occurs from central and eastern Bolivia and extreme southwestern Mato Grosso S through Paraguay (except far east) and Argentina to La Rioja, Buenos Aires, western Uruguay, and western Rio Grande do Sul. This flycatcher inhabits the entire chaco, and extends beyond the chaco mainly to the S,

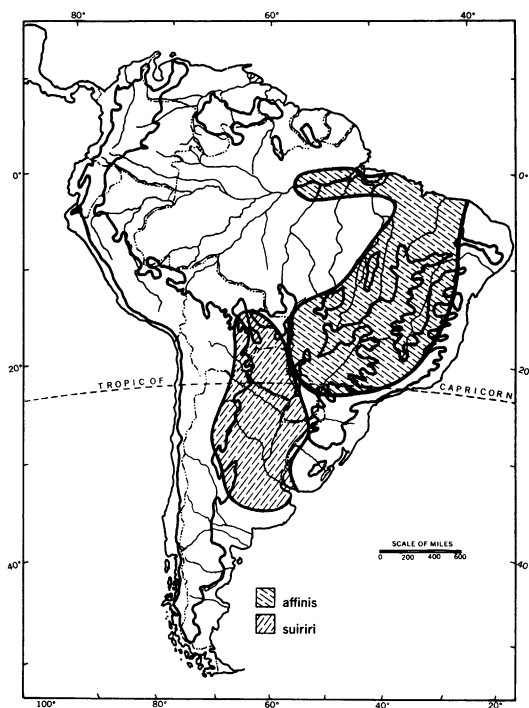


FIG. 52. Range of Suiriri Flycatcher (*Suiriri suiriri*) and its allospecies *S. affinis*. *Suiriri suiriri*, a chaco-pampan-chaco scrub-dry subtropical forest species is parapatric with campo-caatinga *affinis*, and does not appear to interbreed.

but also somewhat to the E, and slightly to the N (central Bolivia) and the W (dry subtropical forest, monte).

Sublegatus modestus
Scrub Flycatcher

Taxonomy. Polytypic species, monotypic genus.

Ecology. Inhabits forest edge, woodland, savanna, and brushland. Territorial. Partly migratory.

Distribution and variation. Southern Middle America and South America. Breeds from Costa Rica to northern Colombia and E and S through Venezuela and the Guianas, eastern Peru, eastern Ecuador, and southeastern Colombia to northern Brazil, including the lower Amazon region (*arenarum* group), and from Maranhão and Pernambuco S through eastern Brazil to Paraná, and Mato Grosso, W to southeastern Peru and northern Bolivia, and thence S through Paraguay to western Uruguay, and northern Argentina S to Mendoza and Buenos Aires (*modestus* group). The two groups are well marked, the southern *modestus* group having a smaller bill, a less gray breast, greener, less gray upperparts, and somewhat smaller size. The southern race *brevirostris*, breeding from Paraguay S, is probably not recognizably distinct from *modestus* (Pinto, 1944). It occurs throughout the chaco and beyond it in the pampas, dry subtropical forest, and wooded eastern Paraguay.

Phaeomyias murina
Mouse-colored Tyrannulet

Taxonomy. Polytypic. No very close congeneric relatives.

Ecology. Small forest, woodland, and savanna flycatcher. Probably not migratory. Builds an open cup nest in trees (Haverschmidt, 1968).

Distribution and variation. Panama and South America. Found from Panama and northern Colombia E and S through the lowlands of all countries to Tucumán, Argentina, northern Paraguay, and southeastern Brazil (São Paulo). Also found in western Ecuador and adjacent northwestern

Peru. *Phaeomyias murina ignobilis* is the subspecies occurring in eastern and southern Bolivia, northwestern Paraguay, and the dry subtropical forest S to Tucumán. This race is distinguished by its relatively short bill and generally pale coloration (especially crown and underparts). It inhabits the northern chaco (northern Paraguayan chaco, Mato Grosso, Santa Cruz chaco) and the western fringe of the chaco from Tucumán to Paraguay, and it extends beyond the chaco mainly to the W.

Camptostoma obsoletum
Southern Beardless Tyrannulet

Taxonomy. Polytypic. Very closely related to, and perhaps conspecific with *C. imberbe* of northern Middle America and the southern United States. These seem to overlap in Costa Rica, but see Meyer de Schauensee (1966, p. 385). *Camptostoma obsoletum* is darker above and more contrastingly colored (more "capped," e.g.) than is *C. imberbe*, but otherwise they are very much alike.

Ecology. Forest, woodland, and scrub flycatcher, abundant generally, and frequenting all strata of trees and bushes, especially thickets. Perhaps partly migratory. Females build a ball-shaped, hanging nest with a side entrance (Haverschmidt, 1968).

Distribution and variation. Southern Middle America and South America. Found in the W from northwestern Peru to Colombia and in the E southward and eastward throughout the lowlands and mountain slopes to Tucumán in western Argentina, western Paraguay, Santa Fe and Entre Ríos in eastern Argentina, and Rio Grande do Sul. The moderately distinguishable *C. o. obsoletum* occurs from western Paraguay and the southern part of Santa Cruz, Bolivia, E to Rio de Janeiro and S to Santa Fe and Rio Grande do Sul. This form inhabits all the pantanal and eastern chaco woodland, and the chaco of northern Paraguay, Bolivia, and Mato Grosso. It extends beyond the chaco to the E. This race is very large, with a short, heavy bill, and is quite green above, but pale. Conceivably this flycatcher reaches the western fringe of the chaco from the dry subtropical forest. It is lacking in most of the southwestern chaco.

FAMILY PHYTOTOMIDAE

Phytotoma rutila
White-tipped Plantcutter
Figure 53

Taxonomy. Polytypic. I consider this species to form a superspecies with coastal Peruvian *raimondii*. These two species both lack the rufous tail pattern characteristic of related *rara*, they have a narrower bill, grayer, less streaked upper parts and a white-tipped tail. *Phytotoma raimondii* differs from *rutila* in having less rufous in the crown, a gray throat, breast, and sides (*rutila* is rufous below), a longer bill, and less dorsal streaking.

Ecology. Social, migratory species, with a serrate bill used in tearing plant buds, leaves, and fruits. Favors woodland edges, and brushland.

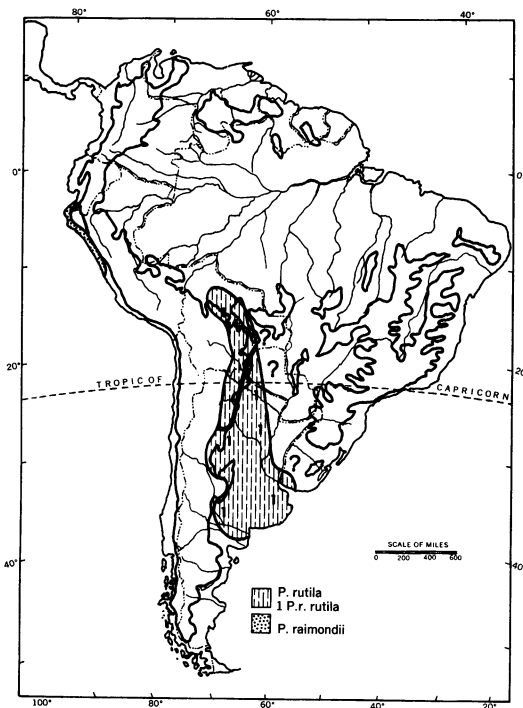


FIG. 53. Range of White-tipped Plantcutter (*Phytotoma rutila*) and its allospecies *P. raimondii*. The former is a species of the pampas, chaco scrub, steppe scrub, dry chaco, and dry subtropical forest, well isolated from *raimondii* of coastal xeric Peru.

Distribution and variation. The superspecies (indeed the family) is endemic in South America. *Phytotoma rutila* is found from central Bolivia S through southern Bolivia and western Paraguay to Mendoza and eastern Río Negro, Argentina, and to western Uruguay. Its status in lowland eastern Bolivia and the Paraguayan chaco is uncertain. It inhabits at least all of the southern chaco and perhaps the northern chaco as well (except Mato Grosso). The narrower-billed, smaller, *P. r. rutila* is the lowland form found in the chaco and S to Río Negro. The Andean slope brushland race *angustirostris* possibly reaches the chaco in Santa Cruz.

FAMILY HIRUNDINIDAE

Tachycineta albiventer
White-winged Swallow

Taxonomy. Monotypic. Its relative, *T. albilinea* of Middle America and western Peru, comprises a superspecies with *albiventer*. These very similar, allopatric species have white in the wings and bear a similarly shaped bill compared with their congeners. *Tachycineta albiventer* has more white in the rectrices, a whiter breast (no gray), more white in the wings, and a somewhat longer bill than *albilinea*.

Ecology. Typical, aerial, insectivorous swallow of forests, woodlands, and savannas, especially near water. Migratory. Nests in cavities in trees. Not highly social.

Distribution. *Tachycineta albiventer* is endemic in South America from northern Colombia E to the Guianas and S over all the lowlands to Jujuy, Argentina, to Chaco and Corrientes in eastern Argentina, and to Paraná. It occurs throughout the northern chaco, S to Formosa and Chaco, but it is lacking in the central and western Argentine chaco, and perhaps in parts of western Paraguay. The chaco forms its southern range limit.

Tachycineta leucorrhoa
White-rumped Swallow

Taxonomy. Monotypic. With *T. leucopyga* it forms a superspecies. The latter breeds from northern Chile and Río Negro to Tierra del

Fuego, and it is slightly smaller in size, bluer (more violet, less blue-green), and the white is restricted to a very narrow area over and in front of its eyes, compared with *leucorroha*. Both are relatively large and white-rumped, with dark cheeks and white in the face, both lack whitish in the bases of the back feathers, and they have no white patches in the wings and tail.

Ecology. Nests in holes in trees, sometimes in houses, and forages in small groups or pairs over open country, woodland edges, water, and forests. Migratory.

Distribution. The superspecies is endemic in southern South America. *Tachycineta leucorroha* breeds in northern Bolivia (possibly disjunctly), and from southern Bolivia, northern Paraguay, and São Paulo S through Uruguay to La Rioja and Buenos Aires, Argentina. It is found in all parts of the chaco except the extreme N (Mato Grosso, Bolivia, northernmost Paraguay), and it occurs S and E from the chaco.

Phaeoprogne tapera
Brown-chested Martin

Taxonomy. Polytypic. Monotypic genus of uncertain relationships.

Ecology. Large and social swallow of open woodland, forest edges, and cultivated regions. Migratory. Nests in cavities, and often in old nests of furnariids.

Distribution and variation. Endemic in South America from northern Colombia, the Guianas, Pará, and Pernambuco S through the lowlands to Mendoza, Córdoba and Buenos Aires, Argentina, and Uruguay. *Phaeoprogne tapera fusca* of eastern Bolivia, Mato Grosso, and Espírito Santo S to Uruguay and Argentina is distinguished from northern *tapera* by its whiter throat and belly, its stronger, darker pectoral band, and the dark spots reach the belly from that band. *Phaeoprogne tapera fusca* inhabits all the chaco and extends beyond it in all directions.

Progne chalybea
Gray-breasted Martin and
Progne modesta
Southern Martin

Figure 54

Taxonomy. Both polytypic. These two mar-

tins form a superspecies with West Indian and possibly (*sinaloae*) Mexican *P. dominicensis* and *P. subis* of North America and Mexico (Mayr and Short, 1970). All are essentially allopatric, replacing one another throughout the Western Hemisphere. It is noteworthy that the temperate extreme species *subis* and *modesta* are darker (ventrally as well as dorsally) than the more tropical species. All may prove conspecific. *Progne modesta* differs from *P. chalybea* in its all blue-black color of males and darker ventral color of females.

Ecology. As others of the superspecies, colonial, local in distribution when breeding. Nest in holes in trees and buildings. Frequent open areas in forests, savannas, pampas or steppes, water-courses, and villages. Migratory.

Distribution and variation. *Progne modesta* is endemic in South America, including the Galapagos Islands, Peru to northern Chile along the west coast, and from central Bolivia S along the Andes to Chubut, and E in the lowlands to Córdoba, Santa Fe, eastern Chaco Province, Entre Ríos, and southern Uruguay. *Progne chalybea* occurs from Middle America, and in South America from northwestern Peru N to Colombia, E from there to the mouth of the Amazon, and S through lowlands of all regions except northern Bolivia to eastern Bolivia, Paraguay, Uruguay, and Argentina S to Santiago del Estero, Tucumán, Córdoba, and northern Buenos Aires. The southern *P. modesta elegans* of Bolivia to southern Argentina is much larger than West Coastal and Galapagos birds, and females have more white on the body (especially the forehead). Southern *P. chalybea domestica* of eastern Bolivia, Mato Grosso, and Rio de Janeiro S to Uruguay and northern Argentina is larger, including the bill, than more northern races of that species. Thus, *P. c. domestica* occupies most of the chaco (Paraguay, Bolivia, Mato Grosso, Formosa, Salta, Santiago del Estero, Chaco, Santa Fe), and *P. m. elegans* occurs sympatrically with *domestica* in the southern chaco (eastern Chaco Province, Santa Fe, Santiago del Estero). The former ranges N and E from the chaco, and *P. modesta elegans* ranges S and W from the chaco. The status of the two forms at the western fringe of the chaco is uncertain. At least some hybridization occurs between *P. m. elegans* and *P. c. domestica*

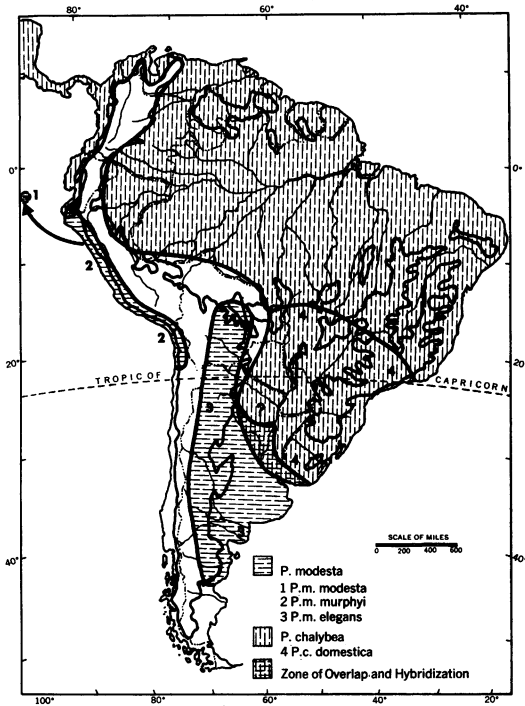


FIG. 54. Range of Southern Martin (*Progne modesta*) and Gray-breasted Martin (*P. chalybea*), two allopecies of four in superspecies *P. subis*. Extent of hybridization between *modesta* and *chalybea* has yet to be established. *Progne modesta* is bird of pampas, chaco scrub, steppe scrub, and dry subtropical forest, barely reaching chaco; there are three isolated races, as shown. *Progne chalybea* is a lowland woodland-forest species. Both martins utilize human dwellings for nesting purposes.

in Córdoba (specimens, AMNH), and probably elsewhere in the area of overlap. Studies of the interactions of these martins are needed, both in Argentina and in northwestern Peru. The local, colonial nesting habits of these martins, habituation among colony members, and the likelihood that birds of a colony migrate together, all would tend to restrict hybridization.

Stelgidopteryx fucata
Tawny-headed Swallow

Taxonomy. Monotypic. Various authors have noted that this species resembles *Stelgidopteryx*

ruficollis, as reflected in its usual position beside the latter in most classifications. Zimmer (1955, p. 18) maintained *Alopocheidon* for *fucata* on the basis of its weaker bill and lack of the "rough wing" compared with *Stelgidopteryx ruficollis*, and he indicated that *Alopocheidon* was a weakly defined genus. It is here merged in *Stelgidopteryx*, rather than being maintained as a monotypic genus.

Ecology. Nests in banks and ranges in forests mainly along streams, in woodlands, pampas, and other types of terrain where nesting sites are available, in loose colonies, or individually, like *ruficollis*. Migratory.

Distribution. Endemic in South America. Disjunct populations occur in northern Venezuela, in mountainous southeastern Venezuela, in eastern Peru, and from northern Bolivia, Mato Grosso, and Minas Gerais S through eastern Bolivia, Paraguay, all southern Brazil, and Uruguay to Mendoza, Córdoba, and Buenos Aires, Argentina. It is found throughout the chaco and beyond it in all directions.

Stelgidopteryx ruficollis
Rough-winged Swallow

Taxonomy. Polytypic. Probably not very distantly related to *S. fucata*.

Ecology. Dependent on banks of earth in which it nests in pairs or loose colonies. Migratory. Found in all types of country affording such banks, but not high in mountains.

Distribution and variation. New World, S to Peru W of the Andes and throughout eastern South America S to eastern and southern Bolivia, western Paraguay, Catamarca in western, and northern Buenos Aires in eastern Argentina, and Uruguay. Birds from eastern Peru, southern Amazonia and Maranhão southward represent *S. r. ruficollis*, a dark form with a dark brown uropygium distinguishing it from other races of the rusty-throated *ruficollis* group (Central, South America). *Stelgidopteryx ruficollis ruficollis* is found in the northern chaco and all the eastern chaco (mainly pantanal); it is absent from the arid parts of the south-central chaco, but may enter the western fringe of the Argentine chaco. From the chaco it extends slightly W, and extensively N and E.

FAMILY CORVIDAE

Cyanocorax cyanomelas

Purplish Jay

Figure 55

Taxonomy. Monotypic. This jay and *C. caeruleus* of southeastern Brazil, Misiones, and eastern Paraguay form a superspecies. Both are similar in pattern, size, and bill shape. *Cyanocorax cyanomelas* is a dull brownish purple version of the azure blue *caeruleus*. These forms, possibly conspecific, may meet in eastern Corrientes and eastern Paraguay.

Ecology. *Cyanocorax cyanomelas* is a flocking species, moving about in small parties, and foraging for all manner of fruits, insects, and other foods. Aggressive, allowing close approach while challenging intruders. Nonmigratory.

Distribution. The superspecies is endemic in south-central South America. *Cyanocorax cyano-*

melas is found from southeastern Peru SE through northern and eastern Bolivia to western Mato Grosso, central and western Paraguay, and Argentina in eastern Formosa to Santa Fe and northern Corrientes. Misiones is cited for this species by Meyer de Schauensee (1966), but this is unlikely, although post-breeding wanderers may reach westernmost Misiones. Extensive field work in eastern Formosa, northern Santa Fe, and northern Corrientes failed to disclose *C. caeruleus*, although *cyanomelas* was common (Short, 1971b). Eastern Chaco Province and eastern Formosa reports of *caeruleus* are suspect, and may represent misidentifications of *cyanomelas* as *caeruleus*; it is possible that *caeruleus* once occurred farther SW along the Parana River when riparian forests were less cutover, but it appears not to do so now. In any event these species are contiguously allopatric, replacing each other without apparent interbreeding, although they may not be in contact.

Cyanocorax chrysops

Plush-crested Jay

Figure 56

Taxonomy. Polytypic. Forms a superspecies with *C. cyanopogon* of Pará and Paraíba S to Goiás, Minas Gerais, and western Paraná. Both species have the same pattern about the eyes, a similar crest, and a similar plumage pattern generally; they often are merged in a single species. *Cyanocorax cyanopogon* differs from *chrysops* in its smaller bill, larger crest, browner, less purple-blue tone, and more white on the back of its head. The interactions of the two species where they meet (Alagoas, where the situation is unclear, possibly with hybridization; Paraná, and possibly Pará) are in need of study.

Ecology. Social, traveling about in small bands in forests and woodlands. Nonmigratory.

Distribution and variation. The superspecies is endemic in eastern South America. *Cyanocorax chrysops* is found disjunctly in the lower Amazon region (northeastern Amazonas, western Pará), in Alagoas, and from northern Bolivia, southernmost Mato Grosso, southern Paraná and São Paulo S to Tucumán in the W, and to Entre Ríos and Uruguay in the E. The southern disjunct range is occupied by *C. chrysops chrysops*, except for Tucumán in the SW, where *tucumanus*

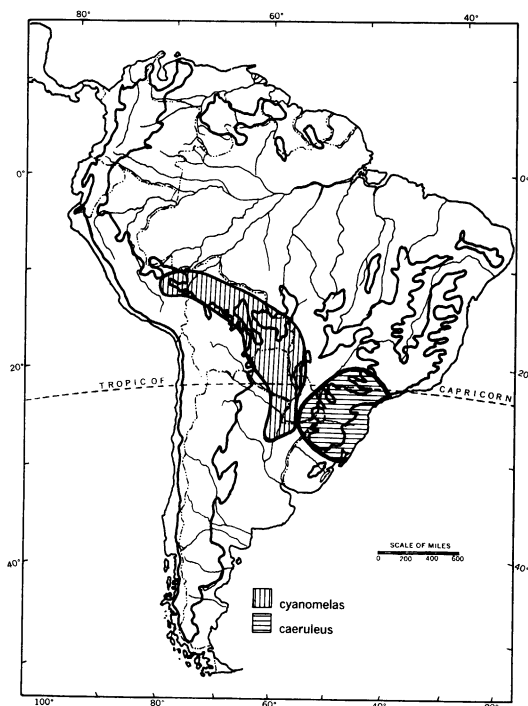


FIG. 55. Range of Purplish Jay (*Cyanocorax cyanomelas*) and its allospecies, *C. caeruleus*. The chaco-east Bolivian *cyanomelas* is parapatric with southeastern Brazilian *caeruleus* with no apparent interbreeding.

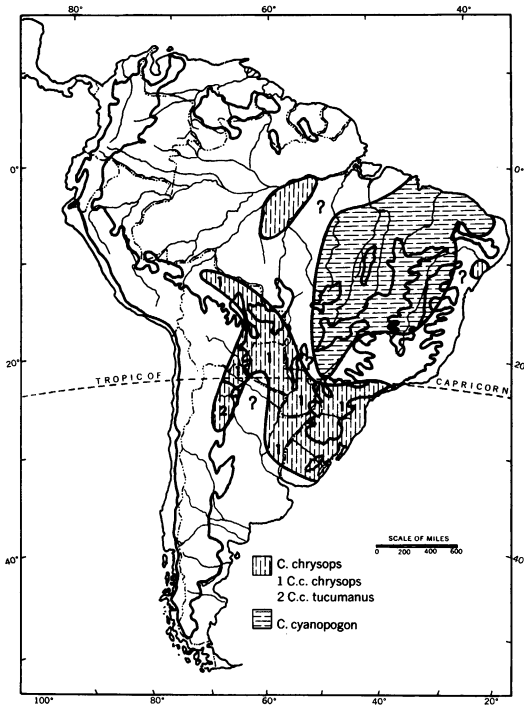


FIG. 56. Range of Plush-crested Jay (*Cyanocorax chrysops*) and its allopecies *C. cyanopogon*. These species apparently are parapatric, but their interactions are unclear. There are three isolates of *chrysops*: a species of southeastern Brazilian forest, one of northern chaco and adjacent campo fringe, and one of dry subtropical forest (southern races). *Cyanocorax cyanopogon* is a bird of campo-caatinga regions.

occurs. The race *chrysops* is brighter and less washed out than *tucumanus*, and it is found in all of the chaco except the central Argentine chaco and northern Santa Fe. It extends slightly W of the chaco, and more extensively NW and E from the chaco.

FAMILY TROGLODYTIDAE

Cistothorus platensis Grass Wren

Taxonomy. Polytypic. Forms a superspecies with *C. apolinari* of the eastern Colombian Andes. These species are very similar in pattern, but *apolinari* is much larger, and is white, not buff, below.

Ecology. Inhabits marshland and grassland. Territorial. Builds ball-nest in grasses. Migratory. Insectivorous.

Distribution and variation. New World S along Andes to Tierra del Fuego. The South American populations are somewhat discontinuously distributed in Colombia, Venezuela, the Venezuelan-Guianan highland region, and from southern Colombia to Tierra del Fuego, extending E over the lowlands to Córdoba, Santa Fe, northern Corrientes and probably adjacent Paraguay, and Buenos Aires. The races occurring in the chaco are the very small *platensis* with its finely streaked crown, and the larger, more heavily streaked *tucumanus*. *Cistothorus platensis platensis* is found in the western pampas and pantanal region N to Corrientes and Santa Fe, E to Buenos Aires, S to Río Negro and W to the Andes of Argentina from La Rioja to Neuquén. *Cistothorus platensis tucumanus* inhabits the southwestern chaco from western Santa Fe through Santiago del Estero to Tucumán, then N to Bolivia and W into the Andes. Thus, *platensis* occurs in the southeastern corner of the chaco and *tucumanus* in the southwestern corner. These regions are somewhat ecotonal in character between pampas and chaco.

?*Thryothorus guarayanus*

Fawn-breasted Wren

Taxonomy. Monotypic. The relationship of this species with *T. leucotis*, a widespread (Panama to eastern Peru, eastern Amazonia, Maranhão, Piauí, Mato Grosso, and Rondonia) wren showing great variation, is clear, and it would be considered conspecific with *leucotis* except for two facts: their ranges approach closely in western Mato Grosso with no indication of interbreeding; and, despite the great geographical variation in *leucotis*, no population of that species approaches the gray-backed condition of *guarayanus*. These species are otherwise very much alike, including the generally streaked face, tail, and other features, and they probably will prove conspecific. A problem is posed by the relationship of *leucotis* to western Ecuador-northwestern Peruvian *superciliaris* and east-Brazilian (Pernambuco, Piauí to Santa Catarina) *longirostris*. Both of these seem closely related to *leucotis*. Both are

long-billed, white-bellied, and either lacking (*superciliaris*) or partly lacking (*longirostris*) streaks on the face. Various races of *leucotis* are either buff-breasted or white-breasted, and face streaking varies from obsolescent to strongly developed; the bill also varies somewhat geographically. The question arises as to whether *longirostris* and *superciliaris* represent a single, now disjunct derivative of ancestral *leucotis*, or whether they evolved independently. These can be considered to comprise a superspecies with *leucotis* and *guarayanus*, but if *superciliaris* and *longirostris* are merged, *guarayanus*, less distinct from *leucotis* than is *superciliaris* from *longirostris*, would have to be merged in *leucotis* and there would be only two allospecies.

Ecology. Virtually unknown. Presumably a thicket-dweller like *leucotis*.

Distribution. Endemic in central South America, from northern and eastern Bolivia to the western edge of Mato Grosso. It is likely to occur in the chaco of Santa Cruz, Bolivia. I have been unable to locate a bona fide Paraguayan specimen of *guarayanus*, but it is possible that this species occurs in northernmost Paraguay, and perhaps the chaco of Mato Grosso.

Troglodytes aedon
House Wren

Taxonomy. Strongly polytypic. Following most authors the *aedon*, *brunneicollis*, and *musculus* groups are treated as conspecific. The species is related to Holarctic *troglodytes* and to northern Andean *solstitialis* (Mayr and Short, 1970).

Ecology. Frequents forest, woodland, and brushland; is found also around habitations, and nests in crevices. Territorial. Migratory.

Distribution and variation. New World in most of the Nearctic and all of Neotropics to Tierra del Fuego and Falkland Islands. The *musculus* group occurs from Mexico S, and it includes the two races inhabiting the chaco. *Troglodytes aedon rex* is found in most of the chaco and beyond to the W (dry subtropical forest, scrub growth in Andes) as far as the high Andes, to the S through monte, chaco scrub, and desert vegetation to Neuquén and Río Negro, and E into eastern Paraguay. This form is paler than eastern *T. a. musculus*, and more rufous (less

gray-brown) than adjacent *bonariae* to the SE. *Troglodytes aedon bonariae* occurs in the south-eastern chaco in eastern Chaco Province and Santa Fe, and thence E to the Atlantic Coast (Río Grande do Sul, Uruguay), and S to Río Negro. Between them these two races occupy the entire chaco, both extending beyond, especially to the S.

FAMILY MIMIDAE

Mimus saturninus
Chalk-browed Mockingbird

Figure 57

Taxonomy. Polytypic. This mockingbird seems to form a superspecies with *M. patagonicus*. Although allied with *M. longicaudatus* and *M. thenca*, *patagonicus* and *saturninus* lack a malar mark, they have little or no dorsal streak-

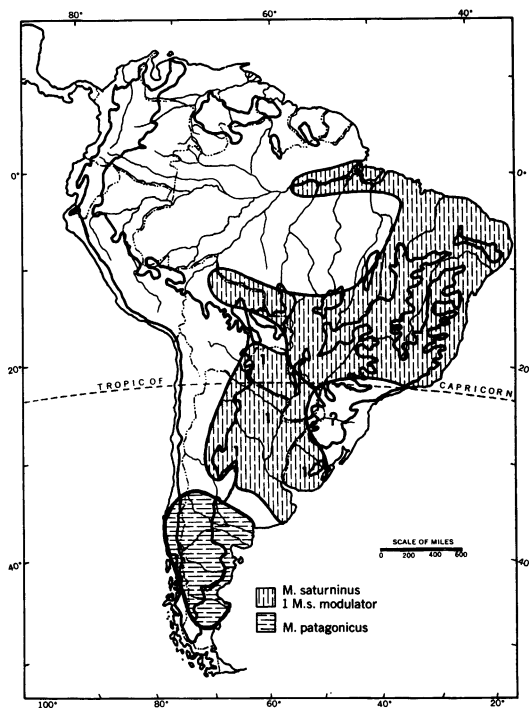


FIG. 57. Range of Chalk-browed Mockingbird (*Mimus saturninus*) and its allospecies, *M. patagonicus*. *Mimus saturninus* is a bird of pampas, chaco, chaco scrub, dry subtropical forest, campo cerrado, caatinga, and Amazonian forest edge.

ing, they lack an auricular patch and have a narrow eye stripe, flank markings are reduced, and their wing patterns are similar and differ from those of *thenca* and *longicaudatus*. *Mimus patagonicus* nests from Neuquén, southern Buenos Aires, and south-central Chile to Santa Cruz, Argentina.

Ecology. Found in woodland edge, thicket, and brushland. Territorial. Nonmigratory.

Distribution and variation. The superspecies is endemic in South America. *Mimus saturninus* occurs from the lower Amazon to Paraíba, and from there S in eastern Brazil through Maranhão, Goiás, and Bahía to Mato Grosso and NW to northern Bolivia; it extends S through Paraguay to Rio Grande do Sul, Uruguay, and northern Buenos Aires, and Mendoza, Argentina. Its status in forested southeastern Brazil is uncertain. Interactions with *M. patagonicus* are not known. Of the four races of *saturninus*, the southern form, *modulator*, is larger than others and it is darker above, especially on the crown. It inhabits Paraguay, southern Rio Grande do Sul, Uruguay, and the Argentine range of the species. This subspecies occurs throughout the chaco, except possibly in Santa Cruz (the species is not known from there), and it extends slightly W and E of the chaco and mainly to the S through the pampas and northern chaco scrub.

Mimus triurus

White-banded Mockingbird

Taxonomy. Monotypic. Forms a superspecies with *M. dorsalis* of the Bolivian highlands and Jujuy, Argentina. These two species exhibit little evidence of dorsal streaking, they have rufous backs, no malar stripes, and tails with a similar, extensively white pattern, compared with other mockingbirds. *Mimus triurus* is smaller, shorter-billed, grayer (less rufous) on the back, and has more white in the wings than *dorsalis*.

Ecology. Common but less conspicuous mockingbird than *saturninus* and frequenting smaller patches of brush in open country, but otherwise occurring in the same habitats. Nonmigratory. Territorial.

Distribution. Superspecies endemic in southern South America. *Mimus triurus* occurs from east-central and eastern Bolivia S through western and central Paraguay and southwestern

Mato Grosso to Corrientes, western Rio Grande do Sul, Uruguay, Río Negro, and Neuquén and is of sporadic occurrence over the Andes in central Chile. It is uncertain whether *triurus* meets *dorsalis* in central Bolivia. *Mimus triurus* is found throughout the chaco, and beyond it slightly to the NW and the W, and farther to the E and S.

Donacobius atricapillus

Black-capped Mockingthrush

Taxonomy. Polytypic species, monotypic genus. No close relatives.

Ecology. Skulking inhabitant of swamps, marshes, and wet areas in grasslands, nesting in the grasses and reeds. Territorial. Nonmigratory.

Distribution and variation. Essentially South American, from eastern Panama E across northern South America and S through the lowlands to eastern Peru, northern Bolivia, eastern Bolivia, central Paraguay, Chaco and Misiones, Argentina, western São Paulo, Goiás, and along coastal eastern Brazil and coastal southeastern Brazil as far as Paraná. The four races are rather weakly distinct, the widespread *atricapillus* being distinguished by relatively unbarred sides. This form occurs from Venezuela S and E throughout the eastern lowland range of the species, except for northern and eastern Bolivia. *Donacobius atricapillus atricapillus* is found throughout the pantanal region of the eastern chaco except in the extreme S (Santa Fe), extending E and N from the chaco in all directions. It is uncertain whether the more barred Bolivian *albovittatus*, or *atricapillus* occupies the Santa Cruz, Bolivia, part of the chaco, along the Paraguay River.

FAMILY TURDIDAE

Turdus rufiventris

Rufous-Bellied Thrush

Taxonomy. Polytypic. The relationships of "robins" are in need of study, based on field investigations. I am uncertain of the relationships of this species.

Ecology. Common about villages, gardens, in light brush, savannas, open woodland, and forest. Territorial. Nonmigratory.

Distribution. Endemic in eastern South America from Maranhão and Paraíba SW through all of eastern and southeastern Brazil to Mato

Grosso, eastern Bolivia, Paraguay, La Rioja, and northern Buenos Aires, Argentina, and Uruguay. Two races are recognized, the southern of which, *rufiventris*, occurs from Goiás and Bahía southward. This form is shorter-billed, but larger than the more northern form. *Turdus rufiventris rufiventris* exhibits clinal variation from E to W in overall tone, such that western (chaco) birds are paler than eastern birds. This race occupies the entire chaco, occurring beyond it W into the dry subtropical forest, S into pampas and chaco scrub, and mainly E and NE.

Turdus leucomelas
Pale-breasted Thrush

Taxonomy. Polytypic. Relationships not clearly established.

Ecology. Inhabits forest and woodland, not coming out of woods. Builds a typical robin's mud-lined nest. Territorial. Nonmigratory.

Distribution and variation. Endemic in South America. Occurs from central, northern, and eastern Colombia E across southern Venezuela, the Guianas, and adjacent Brazil to the mouth of the Amazon, and, continuing SE, from there to Paraíba, and S through Maranhão, Goiás, Piauí, and coastal Brazil to western Mato Grosso (at the Bolivian border), eastern Paraguay, eastern Formosa (personal observ.), northeastern Corrientes, and Paraná; disjunct populations occur in central Peru, and in northeastern Bolivia. *Turdus leucomelas leucomelas*, the larger, longer-billed, browner (less gray) southern race is found from southern Maranhão and Espírito Santo S to Argentina, and Peruvian and Bolivian birds seem to represent this southern race. It is known to occur in the chaco only in eastern Formosa, but it probably is found in other parts of the Paraguay River region (in Paraguay, possibly southwestern Mato Grosso) of the chaco.

Turdus amaurochalinus
Dusky Thrush

Taxonomy. Monotypic. Relationships with other "robins" are undetermined.

Ecology. Rather less conspicuous than *rufiventris*, but occurring in open country about

houses, woodlots, and riparian scrub vegetation, as well as in forests. Migratory in part. Feeds largely on invertebrates.

Distribution. Endemic in South America, from the lower Amazon, southern Amazonia, and northern Bolivia E to Ceará and Bahía, and S through Paraguay and southeastern Brazil to Uruguay, Río Negro, and Mendoza, Argentina. The range N of eastern Bolivia and São Paulo probably represents the winter range of southern birds. It breeds throughout the chaco, its range extending beyond the chaco in all directions, but only slightly to the W.

FAMILY SYLVIIDAE

Poliophtila dumicola
Masked Gnatcatcher

Taxonomy. Polytypic. Relationships in *Poliophtila* largely remain to be established.

Ecology. Woodland and brushland; insectivorous and apparently semi-social when not breeding. Nonmigratory.

Distribution and variation. Endemic in central South America, in the pampas, chaco, campos, and adjoining regions. Found from southeastern Pará, Goiás and western Minas Gerais W through Mato Grosso to eastern and central Bolivia, and S through Paraguay to southern Río Grande do Sul, Uruguay, northern Buenos Aires, San Luis, and La Rioja. Of the three races recognized, the two from the south and west are strongly differentiated from the larger northeastern (central Mato Grosso N and E) *berlepschi*. The latter has white underparts, is grayer above, and has a narrower, less distinct black face patch: the southwestern races are gray below, bluer above, darker generally, the males having large, well-defined black masks. Central Bolivian *saturata* is a large, dark ("saturated") version of the southern *P. d. dumicola*. The latter ranges from eastern Bolivia and southwestern Mato Grosso S through Paraguay and all of northern Argentina except in the high mountains, to Uruguay, Río Grande do Sul, and La Rioja and Buenos Aires. It inhabits all the chaco, extending beyond it only slightly NE, N, NW, and W, and more extensively E and S.

FAMILY MOTACILLIDAE

Anthus lutescens
Yellowish Pipit

Taxonomy. Polytypic. This species appears to have no close relatives in *Anthus*, unless *chacoensis*, known only from wintering birds in Chaco and Formosa, Argentina, and eastern Paraguay, should prove specifically distinct from *lutescens*. If so, it would form a superspecies with it. As no breeding range can be ascribed to *chacoensis*, it is not considered further.

Ecology. This is the only pipit known to breed in the chaco, and it must do so sparingly in cultivated and natural open areas, and especially in the pantanal. Found in fields, savannas, grasslands, including open areas in forested regions. Ground-nesting, social. Migratory. Wandering when not nesting.

Distribution and variation. Panama and South America. Disjunct populations occur in coastal Peru to northern Chile, in the Colombian-Venezuelan llanos, in highland savannas and low open areas of eastern Venezuela and the Guianas, and from the lower Amazon, Maranhão, and Paraíba SW through all of southern Brazil, Mato Grosso, Paraguay, Uruguay, and Argentina S to Mendoza and Buenos Aires. *Anthus lutescens lutescens* is a dark form comprising all three major disjunct populations of eastern South America. It differs from "*chacoensis*" in its hind claw length and tail pattern. *Anthus lutescens lutescens* is found in suitable sites in all parts of the chaco except the NW, and it extends NE, E, and S from the chaco.

FAMILY VIREONIDAE

Cyclarhis gujanensis
Rufous-browed Peppershrike

Taxonomy. Polytypic. Closely related to partly sympatric *nigrirostris*.

Ecology. Woodland edge, and forest treetop species that penetrates savannas and even grasslands if trees are present. Largely insectivorous, gleans methodically. Nonmigratory.

Distribution and variation. Widely distributed throughout the Middle and South American low-

lands, in South America S to northwestern Peru (disjunctly), and south-central Colombia, and E of the Andes throughout all countries (including penetration of the highlands of Peru and Bolivia) to Uruguay and Argentina, where it is found S to northern Buenos Aires, San Luis, and La Rioja. *Cyclarhis gujanensis viridis*, a large, dorsally very gray subspecies (also with restricted brown over the eyes and in the loreal region, and pale underparts with a narrow clear yellow breast band), is found throughout the chaco, and beyond it N to eastern Bolivia, W into the dry subtropical forest, and S in chaco scrub and monte to La Rioja and Córdoba. In the E it meets the distinctive southeastern Brazilian (Espírito Santo to eastern Paraguay, northern Buenos Aires and Uruguay) *ochrocephala* along the Parana-Paraguay rivers, interbreeding with it in southeastern Paraguay (Hellmayr, 1935) and eastern Corrientes (specimens, AMNH). *Cyclarhis gujanensis ochrocephala* is dark in tone and very green above, with a reduced rufous superciliary (not extending behind eye), and it lacks a dark spot on the pale bill.

Vireo olivaceus
Red-eyed Vireo

Taxonomy. Polytypic. The taxonomy used follows that of Mayr and Short (1970), in which West Indian *altiloquus* is treated as a species forming a superspecies with *olivaceus*, and the distinct *olivaceus*, *flavoviridis* (Middle America), and *chivi* groups are considered conspecific.

Ecology. A common, territorial vireo of all types of woodland and forest, including isolated groups of trees in savanna and even pampas. Insectivorous. Migratory.

Distribution and variation. New World from temperate North America to northern Argentina. The *chivi* group inhabits South America in western Ecuador to southwestern Colombia, and from eastern Colombia and northern Venezuela E and S throughout the eastern lowlands and Andean slopes S to northern and eastern Bolivia, Paraguay, Uruguay, and La Rioja, Córdoba, and northern Buenos Aires, Argentina. The *chivi* group is variable, so much so that overlap with Nearctic *olivaceus* occurs in wing formula, and in color features. *Vireo olivaceus chivi* of eastern

Peru, adjacent Amazonian Brazil, northern and eastern Bolivia, western Mato Grosso, the western two-thirds of Paraguay and Argentina E of the mountains S to La Rioja and Buenos Aires, and E to the Uruguay River and Corrientes, overlaps with Nearctic *V. o. olivaceus* in wing formula, it averages brighter yellow on the crissum, and is generally slightly smaller in size; it is larger than surrounding races of the *chivi* group, except for the greener, less gray *V. o. diversus* just E of it. The songs of at least *diversus* and *chivi* are indistinguishable from that of the *olivaceus* group. The *flavoviridis* group enters northern South America; it is distinct by virtue of its bright yellow underparts. *Vireo olivaceus chivi* is the form occupying the chaco, and extending far beyond it to the N, NW and S, as well as W into the forests along the Andes.

FAMILY ICTERIDAE

Molothrus bonariensis Shiny Cowbird

Taxonomy. Polytypic. No close congeneric relatives.

Ecology. A blackbird of open country, woodland edge, and cultivated areas. A brood parasite, laying its eggs in other birds' nests, leaving them to hatch and the young to be raised by foster parents. Partly migratory.

Distribution and variation. Mainly South American, from Panama S to central Peru in the W, and through northern Colombia to the Guianas, and S through eastern Colombia, in the Amazon Valley, and S of Amazonia from Maranhão, Mato Grosso, and northern Bolivia S through all but the eastern corner of Brazil, Paraguay, Uruguay, and Argentina S to Chubut; also in central Chile, where perhaps introduced. Possible gaps occur from eastern Peru to Amapá N of the Amazon, and in much of Amazonia E to Pará. *Molothrus bonariensis bonariensis* occupies the southern and eastern range of the species from Maranhão and Bolivia to Chubut. This race has a medium bill, and females are especially dark-backed, but the subspecies is not well marked. It occurs throughout the chaco, and beyond it in all directions.

Molothrus rufoaxillaris Screaming Cowbird

Taxonomy. Monotypic. Another distinct species, possibly nearest *bonariensis*, but not closely related.

Ecology. A brood parasite chiefly of *M. badius*, its relative. Seems commonest in semi-open country about marshes and flooded grassland. Nonmigratory.

Distribution. Endemic in south-central South America, from southern Bolivia and central Paraguay S to La Rioja, Córdoba, Buenos Aires, Uruguay, and Rio Grande do Sul. It occurs in the southern chaco N to the central Paraguayan chaco and extends S beyond the chaco into the northern pampas.

Molothrus badius Bay-winged Cowbird

Taxonomy. Polytypic. No close relatives among the cowbirds.

Ecology. Unlike the other two species, it lays its eggs in its own nest, although often in abandoned nests of other birds. Found in chaco, caatinga, pampas, and campo areas. Eats insects and seeds. Nonmigratory.

Distribution and variation. Endemic in central South America, in two widely separated areas, the caatinga region from Ceará and Pernambuco, Minas Gerais, and Bahía, and from north-central and eastern Bolivia and western Mato Grosso S through Paraguay to Rio Grande do Sul, Uruguay, and Argentina S to Buenos Aires and Mendoza. All the latter area except montane central Bolivia is occupied by *M. b. badius*. This form, along with *bolivianus* of central Bolivia differs from northeastern Brazilian birds in large size, and grayer rather than brown coloration. *Molothrus badius badius* is slightly smaller and somewhat grayer than *bolivianus*. It inhabits all the chaco and extends beyond it in all directions, but especially to the S.

Sturnella superciliaris Southern Marsh Meadowlark

Taxonomy. Monotypic. Forms a superspecies with *Sturnella militaris* of Panama to the Ama-

zon River region from Peru to Pará. The status of *militaris* and *superciliaris* is in doubt. They may meet in the lower Amazon area, but migration of *superciliaris* perhaps accounts for the "overlap." It is possible that interbreeding occurs someplace in northeastern Brazil. *Sturnella superciliaris* has a shorter bill, but is larger, with longer wings than *militaris*; males have white superciliary stripes lacking in *militaris*. Merger of "*Leistes*" into *Sturnella*, and the treatment of *superciliaris* and *militaris* follows Short (1968). The arrangement of blackbirds with the finchlike relatively unspecialized cowbirds, meadowlarks, and marsh blackbirds (*Agelaius*) placed before more specialized groups follows the suggestion of Short and Bock (1970).

Ecology. Wet grassland and marshland blackbird, territorial when breeding, but forming flocks after the breeding season. Migratory. Forages on ground for insects and seeds. Found in pampas, savannas, and campos.

Distribution. *Sturnella superciliaris* is endemic in South America, breeding from interior eastern Brazil (Maranhão) SW through Goiás and Mato Grosso to eastern Bolivia, eastern and central Paraguay, Rio Grande do Sul, Uruguay, and Argentina S to Buenos Aires, La Pampa, and Mendoza. Its limits in the N and E are unclear, because of the possibly migratory status of many birds. In the chaco the species is found in the entire pantanal region, and it extends NE, E, and S from there. Conceivably it could be expanding its range to include cultivated and irrigated areas in the chaco woodlands.

Agelaius ruficapillus

Chestnut-capped Marsh Blackbird

Taxonomy. Polytypic. Relationships with other congeners are unclear.

Ecology. Inhabits marshland, grasslands, savannas, campos, and woodland edges. Little known. Probably not migratory.

Distribution and variation. Endemic in eastern South America, from French Guiana, Amapá and the mouth of the Amazon to Ceará and Pernambuco and S through interior Brazil to São Paulo, Mato Grosso, Paraguay, the southwestern corner of Rio Grande do Sul, western

Uruguay, and Argentina S to Catamarca and Buenos Aires. The southern race *ruficapillus*, occurring from southwestern Mato Grosso and eastern Bolivia S to Buenos Aires, is larger, more rufous, the male has less chestnut color in the throat and crown, and the female is less yellow below, than the northern form. *Agelaius ruficapillus ruficapillus* inhabits the entire chaco, although it is restricted to swampy and marshy areas, and it extends E, S, and (slightly) W from the chaco.

Agelaius cyanopus

Unicolored Marsh-blackbird

Taxonomy. Polytypic. Related to *A. thilius* and *A. xanthophthalmus* (Short, 1969b).

Ecology. Frequents marshes and swamps in woodlands as well as savannas. Nonmigratory. Forages in marsh grass. Social when not breeding. Nests over water in reeds or bushes.

Distribution and variation. Endemic in South America, with a very discontinuous distribution in Amapá, in Maranhão, in coastal Rio de Janeiro, in eastern Mato Grosso and adjacent São Paulo and Goiás, and from central-northern Bolivia SE through Paraguay to Santiago del Estero, northern Buenos Aires, and Misiones, Argentina. Of the four races, *A. c. cyanopus* includes populations from southeastern Bolivia S, and disjuncts in the Mato Grosso-São Paulo region. This race is strongly marked, males being all black and females showing little black, but instead rufous and brown dorsally, and yellow throughout the underparts. It is found in the eastern chaco, including the entire pantanal, wet areas in the central chaco, and marshes of the northwestern chaco, and extends E and S, and NW from the chaco.

Agelaius flavus

Saffron-cowled Marsh-blackbird

Taxonomy. Monotypic. This species is included in *Agelaius* because its supposed generic ("*Xanthopsar*") characters, including a long, slender bill and more pointed wings (Hellmayr, 1937, p. 184) seem insufficiently marked to separate it as a monotypic genus. *Agelaius* is very variable, and inclusion of "*Xanthopsar*" hardly extends

this variation. It probably is related to the *thilius* group of slender-billed marsh-blackbirds.

Ecology. An open marshland and estero blackbird, with habits like the other marsh-blackbirds. Nonmigratory.

Distribution. Endemic in south-central South America in the wet pampas of Uruguay and southern Rio Grande do Sul, Argentine Mesopotamia (Misiones, Corrientes, Entre Ríos; area between Uruguay and Parana rivers), the southern pantanal region, and southern Paraguay. It enters the chaco only in the southeastern pantanal (Paraguay border S to Santa Fe) and extends E and SE from there.

Pseudoleistes guirahuro
Yellow-rumped Marshbird

Taxonomy. Monotypic. Very closely related to the broadly sympatric *P. virescens*.

Ecology. Highly social, starling-like, frequenting marshes and even small wet patches in grassland. Forages on ground for insects and seeds.

Distribution. Endemic in east-central South America. The more northern of the two species of *Pseudoleistes*, it is found from Goiás and southern Mato Grosso E to Rio de Janeiro and S through eastern Paraguay to Argentine Mesopotamia as far as Buenos Aires, and eastward in the S to coastal Rio Grande do Sul and Uruguay. Its status in eastern Paraná, Santa Catarina, and São Paulo is uncertain. It occurs only in the eastern fringe of the southern chaco, namely in the pantanal area of eastern Formosa to northern Santa Fe, and from there NE, E, and SE.

Pseudoleistes virescens
Brown and Yellow Marshbird

Taxonomy. Monotypic. The southern of the two related and broadly sympatric species of *Pseudoleistes*.

Ecology. As *P. guirahuro*, but more restricted to open country. Ecological relations of these two species would be rewarding. Nonmigratory.

Distribution. Endemic in southeastern South America from southern Rio Grande do Sul to northern Buenos Aires, W to Santiago del Estero and possibly Tucumán (possibly breeding), and N to Corrientes and Chaco provinces. It occurs in the southeastern corner of the chaco, in eastern

Chaco, northern Santa Fe, and adjacent Santiago del Estero, and extends E and SE from there.

Amblyramphus holosericeus
Scarlet-headed Blackbird

Taxonomy. Monotypic genus and species. No close relatives.

Ecology. Blackbird of sedges in marshes and esteros, usually over water. Its habits are little known. Nonmigratory.

Distribution. Endemic in south-central South America. It is found in marshlands from northern Bolivia and eastern Bolivia S largely in the pantanal region and through Mesopotamian Argentina and the wet northern pampas to northern Buenos Aires, Uruguay, and southern Rio Grande do Sul. It is found in the pantanal region of the chaco and in certain marshlands and esteros in the moist eastern chaco woodlands, but is absent in the dry central chaco and in the western chaco. It extends N and S and slightly to the E of that part of the chaco.

Gnorimopsar chopi
Chopi Blackbird

Taxonomy. Polytypic species, monotypic genus.

Ecology. Highly social, inhabits wet areas, including forest edges and swamps, but more often savannas and open country. Feeds in drier areas, as cultivated fields. Nonmigratory, but flocks wander widely after the breeding season.

Distribution and variation. Endemic in eastern South America from Ceará and Maranhão through the campo region to northern Bolivia and S to southern Bolivia, Salta, the pantanal region S to Santa Fe, northern Buenos Aires, and Uruguay, penetrating forested southeastern Brazil to the entire coastal region (N to Alagoas). The southern *G. c. chopi* of western Paraguay and the chaco of Santa Cruz, Bolivia E to Bahía, and SE throughout the southern part of the species' range is much smaller, with a smaller bill, than the northern form. It inhabits the pantanal portion of the chaco, extending W in northern Paraguay, and beyond the chaco to the E and SE. The large northern form, *sulcirostris*, occurs along the Andes S through Tarija to Salta; it may reach the western fringe of the chaco. This race

seems peculiarly disjunct in northern to southern Bolivia and Salta and in northeastern Brazil.

Icterus icterus
Troupial

Taxonomy. Strongly polytypic. Relationships with other *Icterus* uncertain.

Ecology. Inhabits forest and woodland, occurring in dry scrub woodland also. Insectivorous and frugivorous. Nonmigratory.

Distribution and variation. Endemic in South America. Distinct populations occur in north-eastern Colombia and northern Venezuela, in the campo-caatinga region from Maranhão and Ceará to Bahia and Minas Gerais, and in the region from eastern Peru, the middle Amazon, and Guyana S through Mato Grosso to eastern Bolivia, central Paraguay, and Formosa, Argentina. The northern *icterus* group consists of several black-backed, black-headed races, one of which (*metae*) has somewhat reduced black on the back and crown (possibly reflecting previous contact with *croconotus* group). The eastern *jamacaii* is also black-headed and black-backed, but its bill is finer and straighter (not curved) and it has much less white in the wings than does the *icterus* group. The interior *croconotus* group is orange-crowned, and its back is orange, but often with a partial, narrow black band. The southern race of this group, *strictifrons*, occurs in the northern chaco (eastern Paraguayan chaco, Formosa, Santa Cruz, and Mato Grosso) and N to northern Bolivia and northern Mato Grosso. It is paler than northern *croconotus*, but otherwise resembles the latter. The shape of the bill and condition of the wing marks in *jamacaii* suggest relationship with the *croconotus* group; it is possible that it represents an independently evolved form of ancestral *I. icterus*, rather than a direct offshoot of the *icterus* group, but it is uncertain which of these derivations is more likely.

Icterus cayanensis
Epaulet Oriole
Figure 58

Taxonomy. Strongly polytypic. *Icterus chrysocephalus* is considered a species forming a superspecies with *cayanensis*, rather than conspecific with it (see Blake, 1968). *Icterus chryso-*

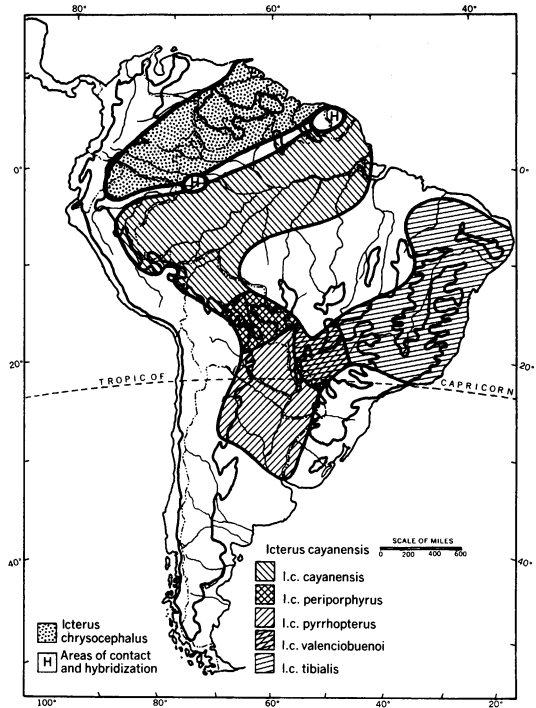


FIG. 58. Range of Epaulet Oriole (*Icterus cayanensis*) shown with various lines, and its allo-species *I. chrysocephalus*, shown stippled. The two hybridize to a degree as yet undetermined in the areas indicated. Three major forms of *I. cayanensis* interbreed through two variable, intergradient "subspecies," as shown. The southern and eastern forms are of chaco-caatinga-campo distribution, but *I. c. cayanensis* is Amazonian.

cephalus ranges from eastern Peru and eastern Colombia to southern Venezuela and the Guianas. It hybridizes with *cayanensis* in French Guiana and the Solimões River region of Brazil (Blake, *op. cit.*). The extent of the interbreeding is not known, but until it is better known the strong variation in *cayanensis* makes it convenient to treat *chrysocephalus* as a species. This oriole differs from *cayanensis* in having a yellow crown and yellow rump.

Ecology. Frequents trees in forests and woodlands, but not most savannas. Territorial. Nonmigratory. Largely insectivorous, foraging in trees and bushes.

Distribution and variation. The superspecies is endemic in South America. *Icterus cayanensis*

occurs from eastern Peru, the Middle Amazon Valley and French Guiana S to the mouth of the Amazon, then W to Bolivia, E through northern Bolivia to Mato Grosso and thence both NE through the highlands and caatinga region to Maranhão and Pernambuco and S through Paraguay to western Rio Grande do Sul, western Uruguay, Buenos Aires, and La Rioja. The southern *pyrrhopterus*, occurring from eastern Bolivia and southwestern Mato Grosso S through the chaco, eastern Paraguay, and to the southern limit of the species' range, is very distinct. It is small and has chestnut (not yellow) wrists and no trace of yellow under the leading edge of the wings (thus differing from other races of *cayanensis* and from *chrysocephalus*). It interbreeds with *I. c. cayanensis* of the Amazon region through the intergradient form *periporphyrus* in central to south-eastern Bolivia, and with *tibialis* of northeastern Brazil through intergradient *valenciobuenoi* in south-central Mato Grosso. The race *pyrrhopterus* occupies all the chaco, and extends to the S, the E, and slightly to the W.

Cacicus chrysopterus
Golden-winged Cacique

Taxonomy. Monotypic. It forms a superspecies with *C. leucorhamphus* of the Andean slopes from Colombia S through eastern Ecuador and eastern Peru to central Bolivia. *Cacicus chrysopterus* is very much smaller than *leucorhamphus*, and it has a darker bill, but otherwise their bills are similar in shape and their color patterns are also similar.

Ecology. Territorial, found in woodland and forest, suspending its nest a distance of up to several meters from tree branches. Insectivorous and frugivorous. Nonmigratory.

Distribution. The superspecies is endemic in South America. *Cacicus chrysopterus* occurs from Tucumán N through dry subtropical forest (and possibly chaco edge) to eastern Bolivia, then across Paraguay and southern Mato Grosso to São Paulo and Espírito Santo, and S through the eastern chaco to northern Buenos Aires and Uruguay. It occurs in the northern chaco, possibly in the western fringes, and throughout the pantanal and moist eastern chaco woodland, and beyond the chaco to the E, N, and W.

Cacicus solitarius
Solitary Black Cacique

Taxonomy. Monotypic. Sympatric with its close relatives.

Ecology. A noisy, territorial cacique of dense tangles and thickets in woodlands, including savannas, often near water. Nonmigratory. Nest very like that of *chrysopterus*.

Distribution. Endemic in South America. Found from southwestern Venezuela S through eastern Colombia, eastern Ecuador, and eastern Peru, E down the Amazon Valley to its mouth and beyond to Ceará, and S through all of central Brazil, northern and eastern Bolivia, and Paraguay, to São Paulo, western Uruguay, Buenos Aires, Santa Fe, Formosa, and Salta, Argentina. It occurs in most if not all of the Paraguayan chaco, the chaco of Santa Cruz and Mato Grosso, the eastern chaco woodland and pantanal S to Santa Fe, and, possibly the chaco fringe in Salta. It extends beyond the chaco to the N, E, SE, and slightly to the W.

Cacicus haemorrhous
Red-rumped Cacique

Taxonomy. Polytypic. Forms a superspecies with *C. uropygialis* of Middle America to northwestern Venezuela, Andean Colombia, and, disjunctly, the eastern Andean slope of Ecuador and northern Peru. Both species are red-rumped, with a blue sheen on black body feathers and a pale bill, and they are similar in size. *Cacicus haemorrhous* lacks a crest and has a larger, more massive bill.

Ecology. Colonially nesting forest, forest edge, and savanna woodland species, foraging on insects and fruits. Nonmigratory.

Distribution and variation. Endemic in South America, occurring disjunctly from southern Venezuela, southeastern Colombia, and eastern Ecuador E through northern Brazil including the middle and lower Amazon to the Guianas, Amapá, and the Amazon delta, and from Bahia and Pernambuco S along the coast to Paraná and SW through Minas Gerais and Goiás to southern Mato Grosso, the Paraguay River of Paraguay and Argentina, and to Santa Fe and Misiones. *Cacicus haemorrhous affinis*, the southeastern disjunct form, is much less glossy blue-black, indeed is

distinctly brownish in tone. It inhabits riparian forests along the Paraguay River, and the lower portions of its major chaco tributaries, and extends E and NE from the chaco.

Psarocolius decumanus
Crested Oropendola

Taxonomy. Polytypic. Sympatric with its congeneric relatives.

Ecology. Colonial, huge blackbird. Forages for fruit and insects in trees. Nonmigratory.

Distribution and variation. Panama and South America in the eastern lowlands from northern Colombia, Venezuela, and the Guianas S through Brazil, eastern Colombia, eastern Ecuador, eastern Peru, and northern and eastern Bolivia to Salta, western Paraguay, eastern Formosa, Corrientes, Misiones, and Santa Catarina; absent from the northeastern corner of Brazil. *Psarocolius decumanus maculatus* is the large, dull brown southern race, occurring from the Amazon and southeastern Peru southward. This form is found in the northern chaco from Salta and the Paraguayan-Bolivian border across northern Paraguay and Santa Cruz, Bolivia, and in the eastern chaco woodland and pantanal S to Formosa. It extends NW, N, and E from that part of the chaco.

FAMILY PARULIDAE

Parula americana
Parula Warbler

Taxonomy. Polytypic. No very close relatives, genus monotypic.

Ecology. Territorial, frequenting both dry woodlands and wet forests and nesting in mosses or other vegetation hanging in trees. Partly migratory.

Distribution and variation. New World, Canada to Argentina. In South America, from Guyana, Venezuela, and northern Colombia discontinuously to western Ecuador and northwestern Peru, and along the eastern base of the Andes from eastern Colombia to central Bolivia, then E across eastern Bolivia, Mato Grosso, and Maranhão S through Paraguay and highland and coastal southeastern Brazil to Uruguay, Buenos Aires, Córdoba, and La Rioja. The southeastern

range E and S of central Bolivia is occupied by *P. a. pitiayumi* of the Neotropical *pitiayumi* group. This race is rather large and gray-blue above, with a weak, diffuse tan breast patch; it is paler than races to the N. It occurs throughout the chaco, barely beyond it to the S and W, and more extensively NW, NE, and E from the chaco.

Geothlypis aequinoctialis
Masked Yellowthroat

Taxonomy. Polytypic. I believe that Middle American *G. poliocephala* forms a superspecies with *aequinoctialis*. These have a very similar bill and a head pattern distinct from other yellowthroats. *Geothlypis poliocephala* has a slightly shorter bill, is browner above with buffy sides, and males have a more restricted face patch. These species barely meet in western Panama.

Ecology. Found in wet or occasionally dry woodland tangles and thickets, the edges of marshes and swamps, brushy areas in savannas and even in the pampas. Territorial. Nonmigratory.

Distribution and variation. Panama and South America, discontinuously in central Colombia, in eastern Colombia to northern Venezuela, in southeastern Venezuela through the Guianas and adjacent Brazil, in the lower Amazon Valley and northeastern Pará, in southwestern Ecuador and northwestern Peru, in southeastern Peru, and from northern Bolivia, eastern Bolivia, central Mato Grosso, Goiás, and Bahía S through southeastern Brazil to Uruguay, through Paraguay to Buenos Aires, and through the chaco and dry subtropical forest to La Rioja and Córdoba. *Geothlypis aequinoctialis velata* is a weak race, characterized by its large size; it occurs in southeastern Peru and throughout the disjunct southern range of the species. It is found in suitable sites in all parts of the chaco and beyond it to the W and S and extensively to the N and E.

Basileuterus flaveolus
Flavescent Warbler
Figure 59

Taxonomy. Monotypic. It forms a superspecies with *B. signatus* of south-central Colombia and eastern Peru along the Andes to Jujuy, Argentina. Their strong similarities were empha-

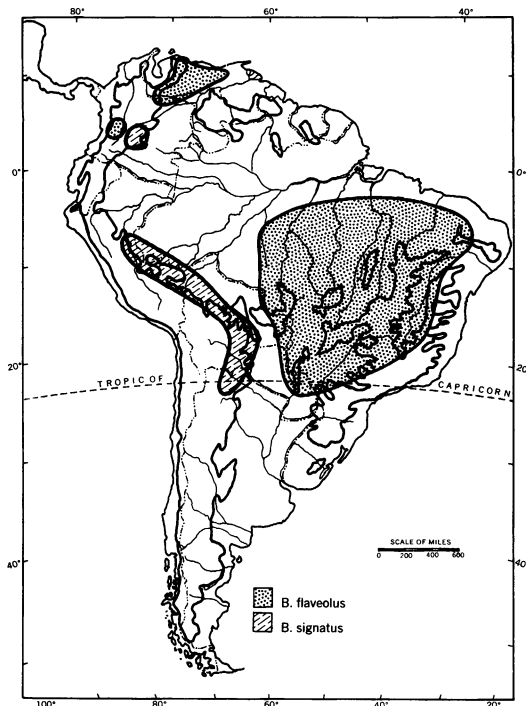


FIG. 59. Range of Flavescent Warbler (*Basileuterus flaveolus*), shown stippled, and its allo-species *B. signatus*, shown with diagonal lines. There are three isolates of the former, and two of the latter. *Basileuterus flaveolus* is a campo cerrado-caatinga-forest edge (also llanos) species, barely reaching the chaco; *signatus* is subandean.

sized by Zimmer (1949, p. 28), although he did not merge them "at present." *Basileuterus flaveolus* has a longer bill and slightly longer wings and tail, it lacks crown stripes (traces in some), and has paler feet and bill and a slightly different wing formula.

Ecology. Woodland, savanna, and campo warbler of the lower shrubbery. Insectivorous. Nonmigratory.

Distribution. The superspecies is endemic in South America. *Basileuterus flaveolus* occurs disjunctly in northwestern Venezuela, in the Cauca Valley of Colombia, and from eastern Amazonia, Maranhão, and Ceará S through the campo region to eastern Bolivia, northern Paraguay, and the Brazilian highlands (São Paulo to Bahia and Pernambuco). It occupies the northeastern chaco woodland and pantanal (Paraguay, Santa Cruz,

Bolivia, and Mato Grosso) and beyond it to the E and N. It is remotely possible that *B. signatus* enters the western fringe of the chaco.

Basileuterus culicivorus
Golden-crowned Warbler

Figure 60

Taxonomy. Polytypic. It forms a superspecies with *B. trifasciatus* of southwestern Ecuador and northwestern Peru; these may be conspecific (Meyer de Schauensee, 1966). Zimmer (1949) pointed out their close affinity. *Basileuterus trifasciatus* resembles *culicivorus* but is gray with a trace of yellow rather than orange-yellow on the crown, and its underparts are grayish white

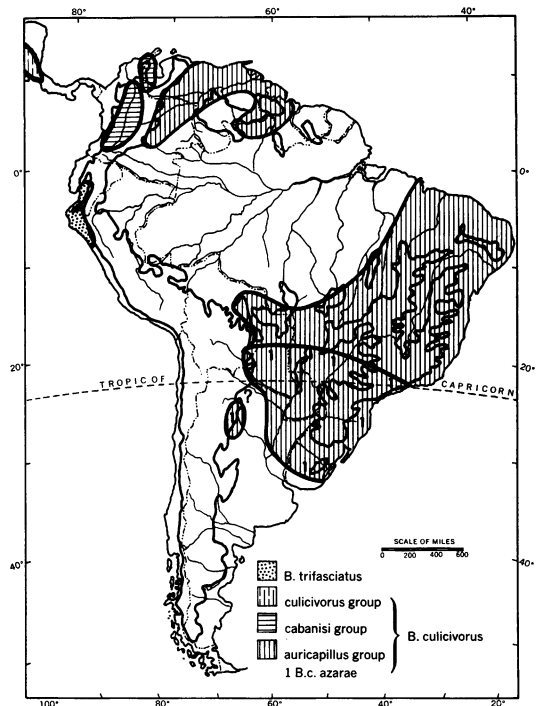


FIG. 60. Range of Golden-crowned Warbler (*Basileuterus culicivorus*) shown with various lines, and its allo-species *B. trifasciatus*, marked with stippling. Note trans-Amazonian distribution of the *auricapillus* group of *B. culicivorus*. Distribution southeastern Brazilian-chaco-dry subtropical forest-campo cerrado-caatinga (southern isolates). Isolate west of chaco may represent Bolivian *B. c. viridescens* rather than *azarae*, but these races probably are not separable.

anteriorly and yellow posteriorly rather than entirely yellow.

Ecology. Frequents woodland and forest undergrowth including edges; found in campos and savannas where sufficiently wooded. Insectivorous. Territorial. Nonmigratory.

Distribution and variation. Middle and South America. In South America it occurs in central Colombia, in northeastern Colombia to northern Venezuela and Guyana, and from north-central Bolivia E across Mato Grosso and Goiás to Maranhão, Ceará, and Rio Grande do Norte, and thence S through all of southern Brazil and Paraguay to northern Uruguay, Entre Ríos, Santa Fe, and Formosa, and, apparently disjunctly to Tucumán (possibly also Córdoba). Three racial groups are recognized, the Middle American *culicivorus* group, the Andean Colombian *cabanisi* group, and the *auricapillus* group of eastern Colombia to Guyana, and in south-central South America. The *auricapillus* group is colored green above and the gular area is usually white, the *cabanisi* group is gray dorsally with a white gular region, and the *culicivorus* group is gray-green above with a yellow gular area (*B. trifasciatus* most resembles the *cabanisi* group). The subspecies *azarae* of Paraguay to Rio de Janeiro and S to Uruguay and Entre Ríos, is duller and browner (less green) dorsally than is more northern, contiguous *auricapillus*; it is possibly less green above than *viridescens* of Bolivia, although probably not separable from it, and darker backed with olive, not gray, margins of remiges as in *segrex* of northern South America. *Basileuterus culicivorus azarae* occupies the Paraguayan chaco, and the eastern chaco woodland generally; it also occurs in the pantanal, including Mato Grosso. *Basileuterus culicivorus viridescens* appears to be the form occurring in the chaco of Bolivia and perhaps in the chaco fringes of Tucumán. The chaco forms the southwestern range limit of the species (except for the Tucumán isolate).

Basileuterus hypoleucus
White-bellied Warbler

Taxonomy. Monotypic. It is closely related to the sympatric *B. culicivorus*.

Ecology. Very little known, apparently in

thickets of scattered woods in the campos region and adjacent forest edges. Nonmigratory.

Distribution. Endemic in east-central South America, from northern Paraguay NE to Goiás, E to Minas Gerais, and SE to São Paulo. It is found only in the northeastern edge of the chaco in the pantanal of Mato Grosso and immediately adjacent western Paraguay (it probably occurs in easternmost Bolivia). It extends E and NE from there.

Basileuterus leucoblepharus
White-browed Warbler

Taxonomy. Monotypic. No close relatives in its genus.

Ecology. A *Seiurus*-like, terrestrial forest and woodland warbler. Territorial. Insectivorous. Nonmigratory.

Distribution. Endemic in east-central South America. Essentially a southeastern Brazilian forest species, occurring from Espírito Santo S along the coast to Uruguay and (formerly?) Buenos Aires, and W through Paraná to eastern and central Paraguay, and Formosa, and Santa Fe, Argentina. Its chaco distribution is limited to wooded areas along the Paraguay-Parana rivers and larger tributaries, and it extends E and SE from there.

Conirostrum speciosum
Chestnut-vented Conebill

Taxonomy. Polytypic. Related to *C. leucogenys*.

Ecology. Tiny, territorial species, foraging, often with tanagers, in treetops about flowers, for nectar, pollen, and insects. Nonmigratory.

Distribution and variation. Endemic in South America. Found in the lowlands E of the Andes, mainly inland except in Venezuela and Guyana, and from there S through eastern Colombia, eastern Peru, eastern Ecuador, the Amazonian region, northern and eastern Bolivia, Brazil E to the mouth of the Amazon, interior Maranhão, Ceará, Pernambuco, Bahía, São Paulo, and to Jujuy, Paraguay, Formosa, Corrientes, and Misiones. From Brazil S of the Amazon and Bolivia southward occurs *C. s. speciosum*, in which males are very pale, with especially pale loreal and subocular areas, and females are paler (lighter green)

than other races. This form occurs in the northern chaco and in the pantanal region of the eastern chaco S to Chaco Province. It extends E and, mainly, N from the chaco.

FAMILY THRAUPIDAE

Tersina viridis Swallow-Tanager

Taxonomy. Polytypic species, monotypic genus. No close relatives.

Ecology. Peculiar, securing insects in flight and foraging in trees for fruit. Nests at least occasionally in holes in the ground (Mitchell, 1957). Perhaps somewhat migratory and given to wandering.

Distribution and variation. Essentially South American, from eastern Panama S to Ecuador in the W, E to French Guiana, and SW from Venezuela through eastern Colombia, eastern Ecuador, eastern Peru, and western Amazonia to northern and eastern Bolivia, and E through Mato Grosso to Maranhão and the entire eastern coast of Brazil, S to Rio Grande do Sul, and inland S to Misiones and central Paraguay; apparently an isolate occurs in the lower Tapajoz River region. *Tersina viridis viridis*, a very large race in which males are notably paler than in other subspecies, occurs from eastern Bolivia and Mato Grosso E and S throughout eastern Brazil, and to Paraguay and Misiones. This form occupies the northeastern chaco, including the eastern Paraguayan chaco (specimens from Lichtenau in AMNH), and adjacent Santa Cruz, Bolivia, and Mato Grosso; it extends N, NE, and E from the chaco.

?*Chlorophonia cyanea* Blue-naped Chlorophonia

Taxonomy. Polytypic. Related to *C. flavirostris*, but not very closely.

Ecology. Not well known, but is a forest species associated throughout most of its range with mountain slopes and hills. Nonmigratory.

Distribution and variation. Endemic in South America, discontinuously distributed in western and northern Colombia and northwestern Venezuela, in southeastern Venezuela, Guyana, and

adjacent Brazil, along the Andes from eastern Ecuador to eastern Bolivia, and from central Paraguay, Misiones, and Rio Grande do Sul NE to Bahía. The southeastern form, nominate *cyanea*, is the bluest of the several races, and the only one in which males are blue-backed; females are bluer also, and males lack yellow on the forehead. This race reaches the Paraguay River in the hill country of central Paraguay, and it probably forages, or even breeds on the western side of that river. It extends E from that area.

Euphonia musica Blue-hooded Euphonia

Taxonomy. Polytypic. It forms a superspecies with Middle American *elegantissima*, with which it is often merged. *Euphonia elegantissima* is buffy rather than yellow below, and its forehead is buff rather than yellow or black; dorsally it is bluer in tone.

Ecology. Inhabits forest treetops, foraging for mistletoe berries. Nonmigratory. Social.

Distribution and variation. *Euphonia musica* occurs in South America and in the West Indies. In South America it occurs disjunctly in the lower Amazon Valley, from southeastern Venezuela to Surinam, in northern Venezuela and eastern Colombia, from central Colombia to western Ecuador and northwestern Peru, and from eastern Ecuador along the Andes to eastern Bolivia, thence E through Brazil to Bahía, and S to Tucumán in western Argentina, to Chaco Province and Corrientes in eastern Argentina, and to Rio Grande do Sul. Of the several races, *aureata*, one of those having a black forehead rather than a yellow forehead, occurs E of the Andes and in most of Colombia. This race inhabits the northern chaco of Paraguay, Bolivia and Mato Grosso, and the eastern chaco in eastern Formosa and eastern Chaco Province. It may occur in the fringes of the chaco in Salta. It extends W, N, and E from the chaco.

Euphonia chlorotica Purple-throated Euphonia

Taxonomy. Polytypic. It seems to have no very close relatives.

Ecology. Found in forest, forest edge, and

savanna, foraging for mistletoe berries, usually in small flocks. Nonmigratory.

Distribution and variation. Endemic in South America. It inhabits the area from eastern Colombia across central Venezuela to the Guianas and Amapá, and from the mouth of the Amazon S through all of southern Brazil to northern Uruguay, Buenos Aires, Córdoba, and La Rioja, and W to the middle Amazon River, eastern Peru, northern and eastern Bolivia, and the dry subtropical forest along the Andes in Argentina. *Euphonia chlorotica serrirostris* is the large southern race (male with a very blue back, female very gray above with a gray breast and abdomen) occurring S from eastern Bolivia, central Mato Grosso, and Rio de Janeiro. This form inhabits the entire chaco, and extends beyond it slightly S, SW, and W, and extensively N and E.

Thraupis sayaca
Sayaca Tanager
Figure 61

Taxonomy. Polytypic. *Thraupis sayaca* forms a superspecies with Middle American and northern South American (Colombia, Venezuela, Guianas S to northwestern and southeastern Peru, southern Amazonia, and the southern fringe of Amazonian forest S of the lower Amazon River in Pará) *T. episcopus*. These conceivably could be conspecific, but the wide disjunction of *sayaca* populations with *episcopus* fully occupying the area between them is indicative of a complex history and suggests that they have attained specific status. *Thraupis episcopus* is bluer (less gray) and shows violet tones in the wings, its crown is paler, and it has a conspicuous blue-violet or white patch on the bend of the wing, which is plain blue in *sayaca*; *T. sayaca* is duller, grayer, it shows green in the blue of the underparts and remiges, and its crown is more contrasting. They meet in Maranhão, northern Bolivia, and northern Venezuela, but their interactions are poorly known (see Meyer de Schauensee, 1966, p. 479).

Ecology. Rather omnivorous. Arboreal, noted feeding on meat hung to dry outside a restaurant in rural Argentina. It is found in forests, woodlands, savannas, and desert scrub vegetation; a

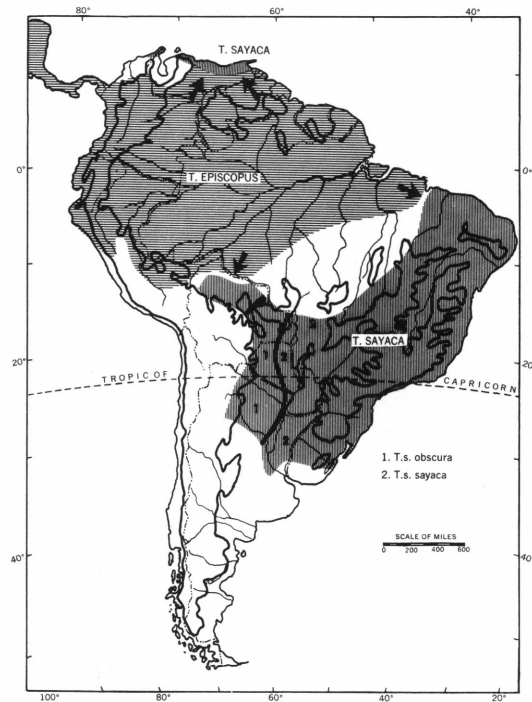


FIG. 61. Range of superspecies *Thraupis sayaca*, with allospecies *T. sayaca* (Sayaca Tanager) in vertical lines, and *T. episcopus* in horizontal lines. Little is known of their interactions at points where they meet (arrows). Possibly *episcopus* is a Middle American invader that has extended between the isolates of *sayaca*. Latter is a forest, woodland, and savanna species of caatinga, chaco, southeastern Brazilian forest, dry subtropical forest, and campo.

cluster of trees about habitations may suffice for a nesting pair. Possibly slightly migratory in S.

Distribution and variation. Endemic in south-central South America. Found from northern Bolivia, central Mato Grosso, Goiás, and Maranhão throughout Brazil to the E and S of these states, and to Paraguay, northern Uruguay, Buenos Aires, Córdoba, and La Rioja. *Thraupis sayaca obscura*, a large, very dark gray form, occupies western Argentina from La Rioja and Córdoba N to Jujuy and Formosa, and beyond to central Bolivia and, presumably westernmost Paraguay. *Thraupis sayaca sayaca*, also large but paler than *obscura*, is found from eastern Chaco

Province, Santa Fe, and Buenos Aires N to the eastern Paraguayan chaco (Orloff, Paraguay, specimens are nearest *sayaca*, showing little influence of *obscura*) and Mato Grosso, and E through Corrientes and Entre Ríos to northern Uruguay, and coastal and interior eastern Brazil N to Maranhão. Thus, the former race occupies most of the chaco, extending beyond it to the W into dry subtropical forest, and N to north-central Bolivia, and *T. s. sayaca* occurs in the eastern chaco and beyond to the SE, E, and NE.

Thraupis bonariensis
Blue-and-yellow Tanager

Taxonomy. Polytypic. No close congeneric relatives.

Ecology. In treetops, woodlands, small patches of trees in savannas, pampas, and highland regions. Feeds on insects and fruits. May be migratory in extreme S.

Distribution and variation. Endemic in South America. It is found in the Andes of Ecuador, coastal and Andean Peru, northern Chile, highland Bolivia, and the Andean slopes and lowlands of Argentina S to Mendoza, La Pampa, and Buenos Aires, and E to Uruguay, Rio Grande do Sul, Misiones, and eastern Paraguay. The western race *darwinii* (Ecuador to western Bolivia and Chile), and eastern *bonariensis* racial group are distinct, but usually are treated as conspecific. *Thraupis bonariensis darwinii* is green-backed, and the *bonariensis* group black-backed, but otherwise they are very similar. *Thraupis bonariensis schulzei* of the *bonariensis* group occupies the southern chaco and beyond it to Jujuy, Salta and the dry subtropical forest and chaco scrub S to Mendoza and La Pampa. Its northern breeding limit is uncertain, but extends at least to Formosa and probably western Paraguay. This form is smaller than eastern (from the Paraguay-Parana rivers and Buenos Aires eastward) *bonariensis*, and females are paler overall and less yellow on the throat.

Piranga flava
Hepatic Tanager

Taxonomy. Strongly polytypic. This tanager forms a superspecies with the Nearctic and northern Middle American *P. rubra*, which is similar in

appearance (males pinker, without orange cast, and females very pale, with no olive) and bill shape (although lacking the notch of *flava's* bill), and which is largely allopatric (see Mayr and Short, 1970).

Ecology. In woodland and forests; also found in savannas and scattered groves of trees in grasslands. Insectivorous and frugivorous. Migratory in part.

Distribution and variation. New World, North America to central Argentina. There are three racial groups, possibly specifically distinct: the *hepatica* group N from Nicaragua, the *lutea* group of southern Middle America and northern and western South America, and the eastern and southern South American *flava* group (Meyer de Schauensee, 1966). The *lutea* group occurs disjunctly in Venezuela and Guyana, in northeastern Colombia, from western Colombia to western Peru, and from eastern Peru to central Bolivia. Races of the *flava* group occur in the Guianas and adjacent Brazil, and from the lower Amazon River, Maranhão and Rio Grande do Norte S through Brazil to eastern and southern Bolivia, Paraguay, Argentina as far as La Rioja, Córdoba, and Santa Fe, and Uruguay. Possible interactions of the two groups in Bolivia and in Guyana are in need of study. *Piranga flava flava*, the southernmost race of the species, is found from south-central Bolivia, Paraguay, and southwestern Mato Grosso S through the range of the species in Argentina, in Uruguay, and in western Rio Grande do Sul. It inhabits all of the chaco and extends beyond the chaco to the W, S, and E.

Tachyphonus rufus
White-lined Tanager
Figure 62

Taxonomy. Monotypic. Forms a superspecies with southeastern Brazilian (Espírito Santo to eastern Paraguay, Misiones, and Rio Grande do Sul) *T. coronatus*. These species are generally similar, males of both lack markings on the thighs, and they lack wide crown patches. *Tachyphonus coronatus* differs from *T. rufus* in having a red crown patch, in the less rufous plumage of females, the gray rather than rufous crown of females, and the greater breast streaking of females. Their ranges are allopatric except for

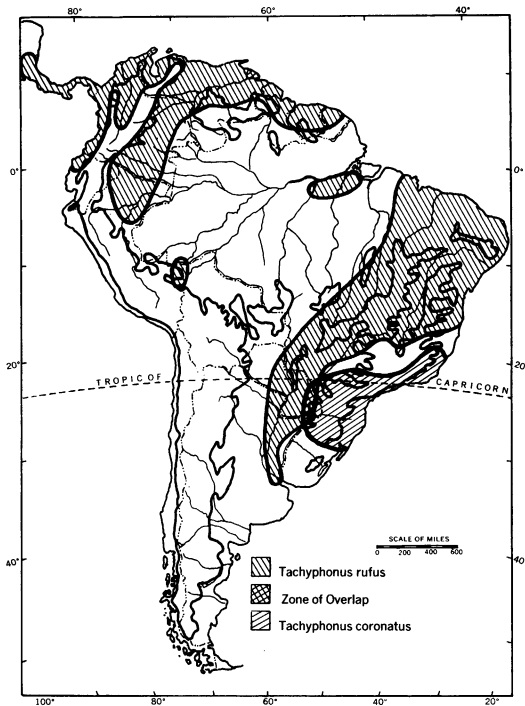


FIG. 62. Range of White-lined Tanager (*Tachyphonus rufus*) and its allospecies *T. coronatus*. These overlap slightly without interbreeding, where indicated. Isolates of *rufus* are undifferentiated. A species of campo, caatinga, and eastern chaco in the south.

slight overlap in southeastern Mato Grosso, eastern Paraguay, and Misiones.

Ecology. Found in forest, woodland and savanna, usually in low trees and bushes, and dense tangles at woodland edges. Nonmigratory. Mainly insectivorous. Territorial.

Distribution. Southern Middle America and South America. It occurs discontinuously from northwestern Ecuador across northern Colombia and Venezuela to the Guianas, and S through eastern Colombia and eastern Ecuador to eastern Peru, in southeastern Peru, in the lower Amazon Valley, and from Maranhão and the eastern corner of Brazil S along the coast to Bahía, and inland to Goiás, Minas Gerais, western São Paulo, Mato Grosso, central and eastern Paraguay, and Argentina from eastern Formosa to Misiones, and S to Santa Fe and northern Buenos Aires. Its chaco range includes the eastern chaco woodland

and pantanal from Mato Grosso and northern Paraguay (but not Bolivia) S to Santa Fe, and the species extends E and NE from there.

Nemosia pileata
Hooded Tanager

Taxonomy. Polytypic. No close relatives.

Ecology. Found in treetops frequenting flowering trees and in wandering bands (in the chaco region these also may include such species as *Hemithraupis guira*, *Thlypopsis sordida*, and *Conirostrum speciosum*), foraging probably on insects (possibly nectar). Found in forests and woodlands. Nonmigratory.

Distribution and variation. Endemic in South America, occurring discontinuously in northern Colombia to northern Venezuela, from eastern Venezuela, the Guianas, and the mouth of the Amazon SW through the middle Amazon Valley to southwestern Amazonia (including northeastern Peru), and S through northern and eastern Bolivia and adjacent western Mato Grosso to Salta in western Argentina, and Formosa and Corrientes in east-central Argentina, and in eastern Brazil from Maranhão and the eastern corner of Brazil S to eastern Mato Grosso and Espírito Santo. *Nemosia pileata caerulea*, a rather weakly characterized subspecies (it is the largest and palest race), occurs from northern Bolivia and western Mato Grosso southward to Salta and Corrientes. This form inhabits the northern chaco from Salta and Tarija across western Paraguay to Santa Cruz, Bolivia, the Mato Grosso chaco, the pantanal and riverine timber along the Paraguay River, eastern Formosa (Espinillo, near Pilcomayo River, observed closely but not collected in September, 1968), and northern Corrientes (Short, 1971b). It extends N and W from the chaco.

Hemithraupis guira
Guira Tanager

Taxonomy. Polytypic. Forms a superspecies with southeastern Brazilian (Bahía to Santa Catarina) *H. ruficapilla*. Both are very different from the other congeneric species (*flavicollis*). They hybridize sporadically in Bahía and in São Paulo (Zimmer, 1947; specimens in AMNH), and perhaps elsewhere in the area where they approach

one another. *Hemithraupis guira* differs mainly in males having a green, yellow, and black patterned head, compared with the rufous head of *ruficapilla*, females are virtually alike, with those of *ruficapilla* being grayer generally.

Ecology. Flocks in treetops, forages on insects and probably nectar and fruits. Nonmigratory.

Distribution and variation. The superspecies is endemic in South America. *Hemithraupis guira* occurs disjunctly in western Ecuador, in southern Colombia, in northeastern Colombia and northern Venezuela, and from eastern Venezuela, the Guianas, southeastern Colombia, and eastern Peru to Piauí, Bahía, western São Paulo, western Rio Grande do Sul, Corrientes, central Paraguay, eastern Bolivia, and in western Argentina S to Tucumán. The southeastern race *fosteri* (S from Bahía to eastern Paraguay), occurs along the Paraguay River (probably western bank; specimens from "Riacho Negro" in western Paraguay are suspect, see Short, 1972a). It is pale dorsally, with a paler black throat and a pale yellow frontal region (males); it is brighter than *H. guira guira*, but paler than *H. g. boliviana*. The latter is dark, especially females (more yellow under tail and on throat; resembling *guira* but yellower and less green); it occurs from western Mato Grosso across northern Bolivia and S to Tucumán. This form occupies the chaco of Santa Cruz, Bolivia, the pantanal of Mato Grosso, and probably the western fringe of the chaco S to Tucumán.

Thlypopsis sordida
Orange-headed Tanager
Figure 63

Taxonomy. Polytypic. Forms a superspecies with *T. inornata* of north-central Peru, and with *T. fulviceps* of northeastern Colombia and northern Venezuela. *Thlypopsis sordida* and *T. inornata* are very similar and may be conspecific; they occur together at Tambillo, Peru (Zimmer, 1947), perhaps due to local or altitudinal movement of one of the putative species. *Thlypopsis inornata* lacks the yellow throat and yellow found on the head of *sordida*, and it is cinnamon-buff, not yellowish below. *Thlypopsis fulviceps* is proportionally similar, with a heavier bill approaching that of *sordida-inornata*; its head is entirely rufous and the rest of its body is gray.

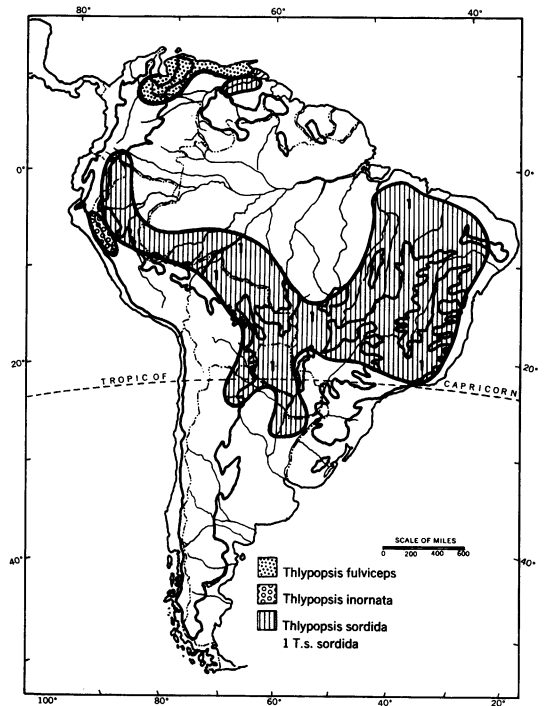


FIG. 63. Range of superspecies *Thlypopsis sordida*, with allospecies as shown, including *T. sordida* (Orange-headed Tanager). These are parapatric, with local (perhaps seasonal) overlap; their interactions are unknown. Note northern isolate of *T. sordida*. Distribution chaco-caatinga-campo cerrado-dry subtropical forest-dry tropical forest.

Ecology. Found in tops of trees in open woodlands, forest edges, forests, and savannas. Nonmigratory. Social.

Distribution and variation. The superspecies is endemic in South America. An isolate occurs in eastern Venezuela; otherwise along Andean slopes and in adjacent lowlands from southern Colombia to southeastern Peru, in western Amazonia, and northern, central and eastern Bolivia, and from there both S through western and central Paraguay to Tucumán in western Argentina, and Corrientes and Santa Fe in eastern Argentina, and E through Mato Grosso to Goiás, eastern Pará, Maranhão, Ceará, interior Bahía, Rio de Janeiro, and Paraná. The entire eastern and southern range of the species NW to Rondonia and northern Bolivia is occupied by the rather

ill-defined *T. s. sordida*, a form somewhat buffier below and with a darker cap than more northern races. This subspecies inhabits the more heavily wooded northern and eastern chaco, from its western fringe in Argentina, across western Paraguay to the pantanal of Mato Grosso and the Bolivian chaco, and S through the eastern chaco woodland and pantanal to northern Santa Fe. It extends slightly W and E and mainly NW and NE from the chaco.

?Cissopis leveriana
Magpie Tanager
Figure 64

Taxonomy. Polytypic species, monotypic genus.

Ecology. Frequents dense shrubbery and the canopy of forests and forest edges, including woodlands in savannas. Nonmigratory. Forages in small groups.

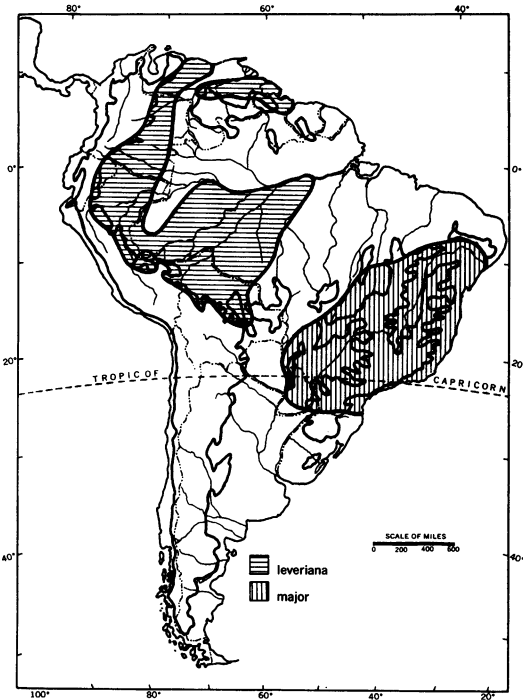


FIG. 64. Range of Magpie Tanager (*Cissopis leveriana*). Barely reaching eastern chaco, southern subspecies has a southeastern Brazilian forest-coating-a-campo distribution.

Distribution and variation. Endemic in South America, from central Venezuela to Guyana, in northwestern Venezuela S through eastern Colombia, eastern Ecuador, eastern Peru, western Amazonia, and Rondonia to northern Bolivia, and from the Paraguay River of Paraguay and southern Mato Grosso E to Goiás, Pernambuco, Bahía, Rio de Janeiro, Santa Catarina, and Misiones. It is known from the Paraguay River near Rosario, Paraguay, and probably at least forages along the western bank in the chaco region.

FAMILY EMBERIZIDAE

Saltator coerulescens
Grayish Saltator and
Saltator similis
Green-winged Saltator

Figure 65

Taxonomy. Both polytypic. These species form a superspecies. *Saltator similis* is like *S. coerulescens* but is paler below, with a white throat and a green back, crown, and wing edges; *coerulescens* is grayer and buffier below, its throat is buff-tinged, and it is gray on the back, crown, and wings. The two are largely allopatric.

Ecology. Found in dense, brushy areas; in diverse woodlands, forests, savannas, and even in grasslands. Nonmigratory. Territorial. In areas where the two species are sympatric, *S. similis* tends to occur mainly in heavy brush bordering rivers.

Distribution and variation. *Saltator coerulescens* occurs in Middle America, and, disjunctly in South America. *Saltator similis* is endemic in central-eastern South America from eastern Bolivia, central Paraguay, eastern Formosa, and northern Santa Fe E to Goiás, southern Bahía, and the Atlantic Coast S to northern Uruguay. In South America, *coerulescens* is found across northern Colombia, and from Venezuela and the Guianas S through the lowlands (except the northwestern edge of Brazil), in the E coastally to the mouth of the Amazon, and inland to western Bahía and Piauí, centrally to Pará, and in the W, to eastern Bolivia, central Paraguay, Corrientes, Entre Ríos, northern Buenos Aires, Córdoba, and La Rioja. The two overlap in western Mato Grosso, easternmost Bolivia, central Paraguay, the eastern chaco of Argentina, Corrientes, and Entre Ríos. *Saltator coerulescens*

coerulescens, the southern race of that species (S from eastern Bolivia and Mato Grosso) is very buffy, like races of the Middle American *grandis* group. This form occupies the entire chaco, and extends beyond it slightly to the W, S, E, and N. *Saltator similis similis* occupies all of the range of that species except the area from São Paulo to Rio Grande do Sul; it inhabits the entire pantanal and eastern chaco woodland, and extends E and NE to Bahía and Goiás. This race is grayish-white below, lacking the strong buffy color of the underparts in southeastern Brazilian *ochraceiventris*.

Saltator aurantirostris

Golden-billed Saltator

Figure 66

Taxonomy. Polytypic. It forms a superspecies with *S. maxillosus* of Espírito Santo to eastern Paraguay, Misiones, and Rio Grande do Sul, and with *S. nigriceps* of southwestern Ecuador and northwestern Peru. The latter is sometimes treated as conspecific with *aurantirostris* (see Meyer de Schauensee, 1966, p. 508), from which it differs in bill shape, its fully black head, and its larger size. *Saltator maxillosus* is darker below than *aurantirostris*, its eye-stripe goes to the bill instead of anteriorly only to the lores, and it has a shorter, heavier bill; these two species interbreed extensively in Corrientes (K. C. Parkes, personal commun.), but I prefer not to merge them until the nature of their interbreeding is clarified.

Ecology. In brushland generally avoiding forest, but found in open woodland, chaco scrub, brushy areas in pampas, and desert scrub. Non-migratory. Forages near or on ground for insects, seeds, and berries.

Distribution and variation. The superspecies is endemic in southern South America. *Saltator aurantirostris* is found from northern Peru SE in the Andes and coastally to northern Chile, and, disjunctly, from northern Bolivia and western Mato Grosso S through eastern and southern Bolivia, and western Paraguay to Mendoza, La Pampa, and northeastern Río Negro, Argentina, Uruguay, and southern Rio Grande do Sul. *Saltator aurantirostris aurantirostris* is a small race, with a narrow black pectoral band, and very tan coloring below (even on the breast); it is found

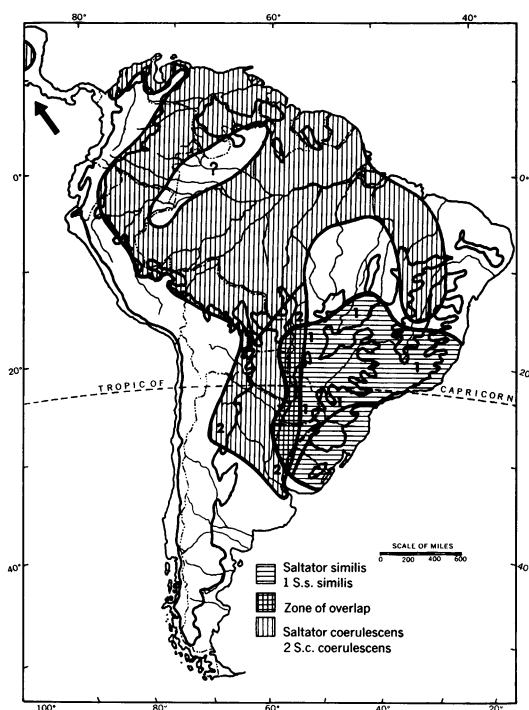


FIG. 65. Range of superspecies *Saltator coerulescens*, including allospecies *S. similis* (Green-winged Saltator) and *S. coerulescens* (Grayish Saltator). Largely allopatric, they overlap as shown. *Saltator similis* is a southeastern Brazilian forest species that extends into edges of chaco, campo cerrado (extensively), and caatinga. *Saltator coerulescens* is a widespread, lowland forest, and scrub woodland species. Their zone of overlap is along eastern chaco border.

from eastern Bolivia and southwestern Mato Grosso through the chaco and part of the dry subtropical forest and the pampas to northern Buenos Aires, Uruguay, Rio Grande do Sul, Corrientes, and the southwestern corner of eastern Paraguay. It inhabits all of the chaco, extending beyond it mainly to the SE.

Gubernatrix cristata

Yellow Cardinal

Taxonomy. Monotypic genus and species, probably related to *Melanodera* and *Phrygilus*.

Ecology. A pampas species, usually found where bushes or small trees are present. Non-migratory. Territorial.

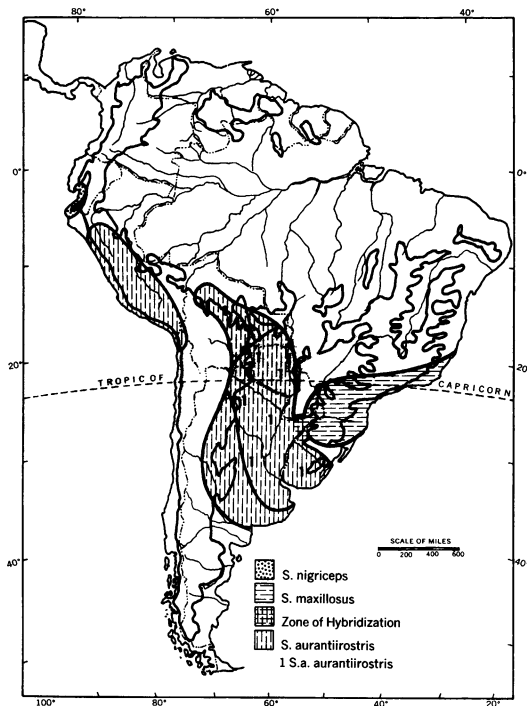


FIG. 66. Range of Golden-billed Saltator (*Saltator aurantirostris*), shown with vertical lines, and its allopecies *S. nigriceps* (stippled pattern), and *S. maxillosus* (horizontal lines). *Saltator aurantirostris* and *S. maxillosus* extensively hybridize where shown. Distribution of *auranti-rostris* is in brushlands of pampas, chaco scrub, chaco, steppe scrub, and dry subtropical forest (southern isolate). Note its allopecies are in xeric scrub (*nigriceps*) and moist subtropical forest (southeastern Brazil, *maxillosus*).

Distribution. Endemic in the pampas region of southern South America, from southern Rio Grande do Sul, Corrientes, and northern Santa Fe S to La Pampa and Río Negro. It occurs mostly SE of the chaco, barely reaching western Corrientes and northern Santa Fe.

Paroaria coronata
Red-crested Cardinal

Taxonomy. Monotypic. Forms a superspecies with *P. dominicana* of Maranhão and Ceará through the caatinga to Minas Gerais. These both have a heavy bill and gray on the back, and unlike other species of *Paroaria* they have white

spots on the upper back. *Paroaria coronata* is gray rather than black on the back, and its white spots are restricted to shafts of the upper back feathers; it has gray rather than black wing coverts, less white in the wing, and a larger, more orange crest.

Ecology. Brushy area and woodland edge finch of the chaco, the pampas, and adjacent regions. Nonmigratory. Eats seeds and insects.

Distribution. The superspecies is endemic in South America. *Paroaria coronata* is found from northern Paraguay, southwestern Mato Grosso and southern Bolivia S to southern Rio Grande do Sul, Uruguay, northern Buenos Aires, La Pampa, and Mendoza. It is found in all the chaco except the northern fringe (Bolivian chaco and Paraguay-Bolivian border), and it extends W, S, and SE from the chaco. There is a north-south cline of increasing size in *P. coronata*, such that chaco birds tend to be small (*P. c. "schulzei"*), but I find that they overlap with southern birds too much to merit racial status.

Paroaria capitata
Yellow-billed Cardinal
Figure 67

Taxonomy. Polytypic. *Paroaria capitata*, *P. baeri* (central Goiás, northeastern Mato Grosso), and *P. gularis* (northern Venezuela, eastern Colombia, eastern Ecuador, eastern Peru, and northern Bolivia, E to the S of the Amazon, and then NE to the Guianas, E to the Amazon Delta, and SE to northwestern Goiás and Pará) form a superspecies. *Paroaria capitata* has a pale bill, a black rear of the throat, and black traces in the red ear coverts. *Paroaria gularis* has a half-black bill, a red head, black throat, and a black ear patch in some races. *Paroaria baeri* is melanic, the red of the head being reduced at the expense of black (blue-black) to the malar region, forehead, and a patch on the crown; the red overlays black in these areas. The last species has a black bill. Paynter (1970) indicated that the three species may be conspecific.

Ecology. *Paroaria capitata* is a brushland species, but it seems to require some tree cover, unlike *P. coronata*. Nonmigratory.

Distribution and variation. The superspecies is endemic in South America. *Paroaria capitata* is

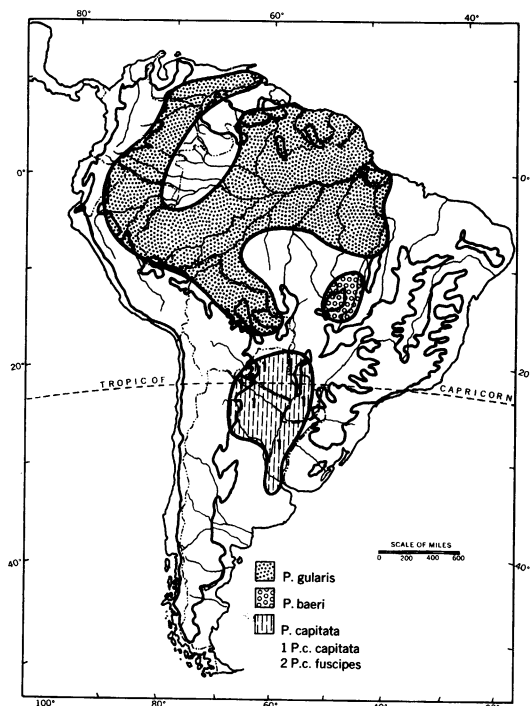


FIG. 67. Range of Yellow-billed Cardinal (*Paroaria capitata*), its campo allospecies *P. baeri*, and its Amazonian-Orinocan allospecies *P. gularis*. *Paroaria capitata* mainly is a chaco species, occurring also in immediately adjacent areas.

found from southwestern Mato Grosso, western Paraguay and southern Bolivia S through northern Argentina to Tucumán, Santa Fe, and Buenos Aires. Two weakly defined races are recognized, *capitata* through most of the species' range, and the smaller, darker-legged *fuscipes* of Tarija, Bolivia. *Paroaria capitata capitata* occurs in all but the northernmost chaco (Bolivia and adjacent northern border of Paraguay), and the western chaco near Tarija, where *fuscipes* probably occurs. It extends W into the dry subtropical forest, E into eastern Paraguay and Argentine Mesopotamia, and slightly SE (to Buenos Aires).

Pheucticus aureoventris
Black-backed Grosbeak
Figure 68

Taxonomy. Polytypic. I consider northern Middle American *chrysopeplus* and southern Middle American *tibialis*, and northwestern

South American (disjunctly in northern Venezuela, in northeastern Colombia and adjacent Venezuela, and in southern Colombia S in the Andes to southern Peru) *chrysogaster* to form a superspecies with *aureoventris*. The first three species are often merged in one (*chrysopeplus*). However, the strong divergence of *tibialis*, its occurrence between the similar *chrysopeplus* and *chrysogaster*, and apparent sympatry of *chrysogaster* and *aureoventris* suggest that they are all best treated as species. *Pheucticus tibialis* is essentially not sexually dimorphic in pattern; its tail is black, its back is mixed yellow and black, and its head and throat are dusky and yellow, with a dusky loreal area. *Pheucticus chrysopeplus* is sexually dimorphic; it has (males) several white areas in the wings, its tail is white-spotted, and it

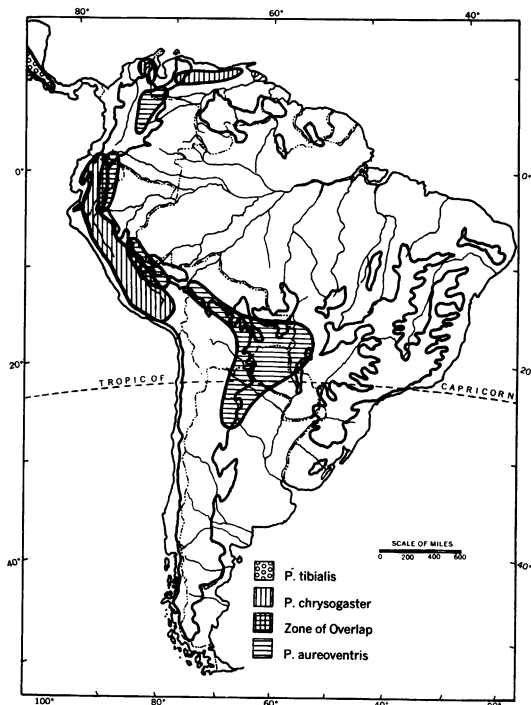


FIG. 68. Range of Black-backed Grosbeak (*Pheucticus aureoventris*) and its allopatric species *P. chrysogaster* and *P. tibialis* (see text). Note isolates of *aureoventris* (mainly subandean), and of *chrysogaster* (more montane), and areas of overlap between these species. *Pheucticus aureoventris* is an Andean subtropical forest species that has extended into northern chaco and chaco-campo ecotone.

is yellow or gold below, including the throat, and on the head. Females of this species are streaked-backed and brown-winged. *Pheucticus chrysogaster* is very much like *chrysopeplus*, but is maintained as a species because of intervening *tibialis*. It differs from *chrysopeplus* in its smaller size, smaller bill, blacker back, less white-tipped tail, and less strongly dimorphic females. *Pheucticus aureoventris* is sexually dimorphic, males being mainly black, including the head and throat, and females being brown, with some streaking in most races (in *P. a. uropygialis* females are very like males). Like *chrysogaster* and *chrysopeplus*, it has white spots in the tail, which are much reduced in females. *Pheucticus aureoventris* is sympatric with *P. chrysogaster* in the Andean slopes of eastern Peru and eastern Ecuador (although they are largely separated ecologically where they occur close together).

Ecology. The superspecies shows a strong tendency to occur in xeric, open woodland with underbrush. The great part of the populations of these species are associated with mountainous areas. There may be some migration, at least downslope.

Distribution and variation. *Pheucticus aureoventris* (and *P. chrysogaster*) is endemic to South America. It occurs discontinuously in Andean eastern Colombia, in southeastern Colombia to northeastern Peru, in southeastern Peru, and from the Andes of north-central Bolivia S along the Andes to Catamarca, Argentina, and E in the lowlands to Salta, western Paraguay, eastern Bolivia, and western Mato Grosso. The southern disjunct population (Bolivia, and to the S and E) is *P. a. aureoventris*, which is distinguished by reduced white (wings, tail) and a black (rather than a yellow, or black and yellow) rump. This form is found in the northern and northwestern chaco from Mato Grosso through the Bolivian and Paraguayan chaco to Salta and Tucumán, and it extends mainly W and NW from the chaco.

Cyanocopsa cyanea
Ultramarine Grosbeak

Figure 69

Taxonomy. Polytypic. It forms a superspecies with Middle American *parellina*. Its pattern is like that of *parellina*, from which it differs by its larger size, including a heavier bill, and duller

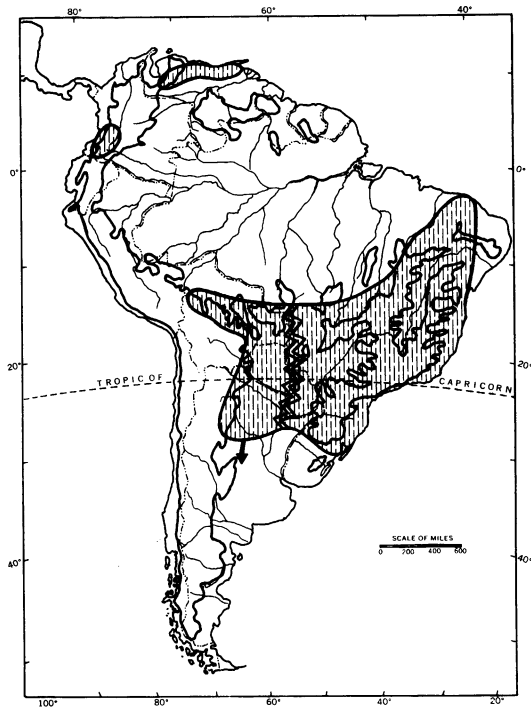


FIG. 69. Range of Ultramarine Grosbeak (*Cyanocopsa cyanea*). Southern isolate includes a western race, *argentina*, that intergrades (zig-zag lines) in eastern chaco with eastern subspecies, *sterea*. Arrow indicates sporadic occurrence southward. A southern brushland species, of caatinga, campo cerrado, southeastern Brazilian forest, chaco, and dry subtropical forest.

coloration overall (muted blues), especially below. Both are smaller billed than related *cyanoides*, with which each is sympatric; their females are paler ventrally than those of *cyanoides*.

Ecology. Found in thickets in woodlands and forests. Forage near ground for insects, seeds. Nonmigratory.

Distribution and variation. Endemic in South America. Isolated populations occur in northern Venezuela, and in southern Colombia. Otherwise, it is found from north-central Bolivia S along the Andes to San Luis, Argentina, and E to Mato Grosso, Goiás, Ceará, Bahía, Rio de Janeiro, and the Atlantic Coast S to Rio Grande do Sul. *Cyanocopsa cyanea argentina*, a large, very heavy-billed race (males dull in color, females very pale below and with a strong rufous tone), occurs from central Bolivia and western Mato

Grosso S through the chaco and dry subtropical forest to San Luis, Córdoba, and Santa Fe, and perhaps sporadically farther. It extends E to western Mato Grosso and the Paraguay-Parana rivers. Birds from the eastern chaco tend toward the more eastern race *sterea*.

Volatinia jacarina
Blue-black Grassquit

Taxonomy. Polytypic species, monotypic genus.

Ecology. Generally a bird of brushy grasslands, shrubbery in edges of forests, woodlands, riparian desert vegetation, and cultivated areas (gardens, villages). Forages in grasses for seeds and insects. Nonmigratory.

Distribution and variation. Widespread from Mexico to Argentina. In South America it occurs S to northern Chile along the Pacific Coast, and E of the Andes, from Colombia, Venezuela, and the Guianas throughout the lowlands S to São Paulo, eastern Paraguay, Buenos Aires, San Luis, and Mendoza. The southern *V. j. jacarina* inhabits the area S of northern Bolivia and Maranhão, and it is larger in size, and females are buffier brown than in other races. This form occurs throughout the chaco and beyond it slightly to the E and W, and extensively S, and of course, N.

Sporophila collaris
Rusty-collared Seedeater
Figure 70

Taxonomy. Polytypic. Relationships are not clear in this difficult genus.

Ecology. One of the several seedeaters of this genus inhabiting brushy grassland and savannas in the tropics and fringes of the tropics; social, perhaps even when breeding. Eats seeds and insects. Not known to be migratory.

Distribution and variation. Endemic in central South America, from northern Bolivia, Mato Grosso, and Goiás, SE to Espírito Santo and Rio de Janeiro, and S to São Paulo, central Paraguay, and Argentina S to La Rioja and Buenos Aires; E to Corrientes and western Uruguay in the S. *Sporophila collaris melanocephala* occurs from southwestern Mato Grosso and northern Paraguay southward. It is less black (throat, back) and more rufous (underparts, neck) than other

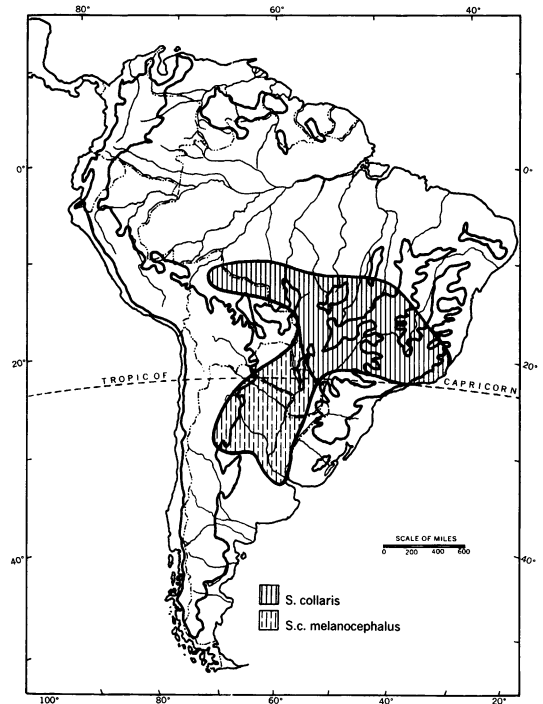


FIG. 70. Range of Rusty-collared Seedeater (*Sporophila collaris*). Southern subspecies occupies chaco and pervades immediately adjacent areas. A brushland species of chaco, campo cerrado, dry subtropical forest, and northern pampas, as well as other, ecotonal areas.

races. This form occupies all of the chaco except the northwestern corner (Bolivian chaco, and northwestern Paraguay) and extends beyond the chaco to the E and W and, mainly, S.

Sporophila lineola
Lined Seedeater

Taxonomy. Polytypic. Its relationships are unclear.

Ecology. Little known grassland and savanna seedeater also found in clearings in forested areas. Nonmigratory. Granivorous and insectivorous.

Distribution and variation. Essentially endemic in South America. Found from northern Colombia, from Trinidad and Tobago, and from northern Venezuela S through the Guianas, eastern Colombia, eastern Ecuador, northeastern

Peru, northern Brazil, all but southwestern Amazonian Brazil, and central and eastern Brazil S to eastern (but not northern) Bolivia, western Paraguay, Tucumán, Santa Fe, Mato Grosso, and São Paulo. *Sporophila lineola lineola* (extensive white in male's crown) is found from Venezuela and the Guianas S through the range of the species, with "*bouvronides*" as a morph in the northern part of its range (Meyer de Schauensee, 1966, p. 508). *Sporophila lineola lineola* inhabits all of the chaco, which forms the southern extreme of the species' range; it extends slightly W into dry subtropical forest and mainly N and NE.

Sporophila caerulescens
Double-collared Seedeater

Taxonomy. Polytypic. Its relationships in *Sporophila* are not clear.

Ecology. Brushland, grassland, and forest clearing seedeater. Nonmigratory.

Distribution and variation. Endemic in South America. The most southerly occurring seed-eater, found disjunctly in the lower Amazon Valley, and from northern Bolivia, southern Pará, Goiás, and Bahía S through southern Brazil to Uruguay, Buenos Aires, and sporadically to Chubut (Lowery and Short, 1969), and inland to eastern Bolivia, Paraguay, La Pampa, and Mendoza. *Sporophila caerulescens caerulescens* is the race occupying the major portion of this range, except for the NW corner (north-central Bolivia) and the NE corner (Bahía). This form is grayer and less black (males) than other races, and it lacks a cap. It occurs throughout the chaco, and beyond it in all directions, but especially to the N, E, and S.

Sporophila leucoptera
White-bellied Seedeater

Taxonomy. Polytypic. Relationships uncertain.

Ecology. Inhabits savanna grassland, forest, and woodland edge. Forages for seeds and probably insects in grasses and shrubbery. Nonmigratory.

Distribution and variation. Endemic in South America. Found from the mouth of the Amazon throughout eastern and southeastern Brazil to São Paulo, and W to Goiás, Mato Grosso, and

northern and eastern Bolivia; S to central Paraguay and northern Santa Fe. The northern Bolivian *S. l. bicolor* is strongly differentiated from the other three races, being glossy black rather than pale gray dorsally, but its pattern, including a white rump, is similar. *Sporophila leucoptera leucoptera* is the south-central race of the *leucoptera* group, differing in its larger size and the paler tan color of females compared with northeastern races. This form occupies the entire eastern chaco pantanal and open areas in the eastern chaco woodland from Santa Fe N to Santa Cruz, Bolivia; it extends mainly NE from the chaco.

Sporophila hypoxantha
Tawny-bellied Seedeater

Figure 71

Taxonomy. Monotypic. I have provisionally included within this species *S. "ruficollis"* and *S. "palustris."* *Sporophila ruficollis* is identical with *S. hypoxantha* except for the presence in males of a black patch covering the throat, upper breast, malar region, and ear coverts, and for slightly larger size of such males. I am unable to separate females of the two forms by size classes, or color pattern; they are indistinguishable. This form overlaps with *hypoxantha*, except in the extreme E (where only *hypoxantha* males are known), and in the extreme W, where only *ruficollis* seems to occur. In the intervening area both forms are found together, often in association, in wet grasslands, esteros, and edges of marshes. *Sporophila palustris* is known only from a small area from central Paraguay to the Uruguay River region of Rio Grande do Sul, Uruguay, and Entre Ríos, Argentina. It is found in the same habitat, and has been collected with *ruficollis*. Females cannot be distinguished from those of *ruficollis-hypoxantha*, and males differ only in having the upper breast, throat, malar region and ear coverts white instead of cinnamon or black. I consider the species polymorphic, with rufous-throated, black-throated, and white-throated phases (males), although field studies are needed to clarify their status. *Sporophila hypoxantha* (rufous-throated phase) is often merged in *S. minuta*, but these differ in color, and in size (females of *minuta* lack white wing

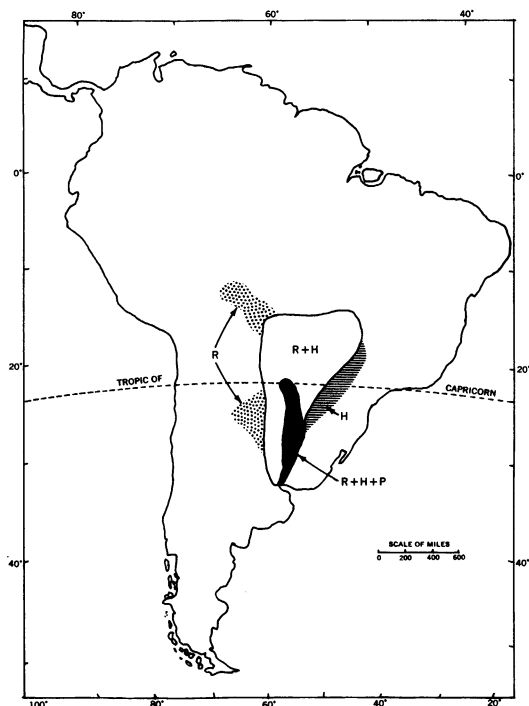


FIG. 71. Range of Tawny-bellied Seedeater (*Sporophila hypoxantha*), including *S. "ruficollis"* (R) and *S. "palustris"* (P), provisionally treated as morphs of *hypoxantha* (H). The *palustris* form occurs rarely, and totally within range of *hypoxantha* and *ruficollis*, as indicated in black. Latter two overlap greatly, but *hypoxantha* extends east of *ruficollis* (horizontal lines) and *ruficollis* occurs alone (stippling) west of *hypoxantha* (see text). Species frequents wet areas of chaco, campo, dry subtropical forest, and northern pampas.

marks of *hypoxantha*; see Short, 1969c). It is certain that *ruficollis* and *palustris*, if not conspecific with *hypoxantha*, are related most closely to it, and it seems that *S. cinnamomea* and perhaps *S. bouvreuil* are related to *hypoxantha* independently from *minuta*.

Ecology. The two widespread forms are found in flooded pampas, marsh edges, and wet places in savannas. The white-throated form is found in "pajonales," and has been seen associated with "*ruficollis*" in Uruguay (Vas-Ferreira and Gerzenstein, 1961). Nonmigratory, but may wander after breeding, particularly as wet areas dry up in fall and winter.

Distribution. Endemic in South America, from northern Bolivia E to Goiás, and S to São Paulo, Paraná, western Rio Grande do Sul, western Uruguay, northern Buenos Aires, Córdoba, and Tucumán. The black-throated ("*ruficollis*") form occurs within this area except in the extreme E (western Paraná, Misiones, western Rio Grande do Sul). The rufous-throated form (typical *hypoxantha*) occurs throughout the above range except in the far NW (northern Bolivia), and the SW (Tucumán, Salta, Santiago del Estero—but it is known from Jujuy, represented by a specimen in the Museum of Comparative Zoology at Cambridge), where only *ruficollis* has been observed. The white-throated phase ("*palustris*") has been taken in south-central Paraguay, southwestern Rio Grande do Sul, eastern Entre Ríos, and western Uruguay (there is a sight record for southeastern Uruguay, where neither of the others has been reported). Thus, rufous-throated and black-throated forms are found in most of the chaco, only the black-throated phase is found in Santiago del Estero and Salta, and the white-throated morph has been taken only once in the eastern chaco of Paraguay. The species extends beyond the chaco mainly to the SE and NE.

?*Sporophila hypochroma*
Chestnut Seedeater

Taxonomy. This seedeater, which is monotypic (Short, 1969c), forms a superspecies with *S. cinnamomea* of eastern Paraguay, Mato Grosso, and Goiás. It seems closely related to *S. hypoxantha*. *Sporophila hypochroma* is very likely to be conspecific with *cinnamomea*, as Meyer de Schauensee (1966) has suggested. In fact, these forms differ only in the color of the back, which is gray in *hypochroma* and chestnut-rufous, as the rump, in *cinnamomea*. The finding of *hypochroma* in Corrientes (Short, 1969c), close to Villarica, southeastern Paraguay, where *cinnamomea* has been taken suggests that they may represent color phases. They are of the same size, and slightly smaller than *hypoxantha*, from which they also differ by their deeper chestnut underparts, rump, and (*cinnamomea*) back; females are virtually indistinguishable.

Ecology. Little known. The Corrientes male (Short, 1969c) of *hypochroma* was taken in a

grassy estero, over standing water, habitat like that of *hypoxantha*. Nonmigratory.

Distribution. The superspecies is endemic in central South America. *Sporophila hypochroma* occurs in western Santa Cruz and in southern Beni, Bolivia, and in northern Corrientes, Argentina. *Sporophila cinnamomea* is found in eastern Paraguay (and Mato Grosso and Goiás). The former probably occurs in the chaco between Bolivia and northeastern Argentina, and the latter possibly may do so. *Sporophila hypochroma* is monotypic; the British Guiana record (see Meyer de Schauensee, 1966) of *S. h. "rothii"* represents a hybrid of *S. minuta* × *S. castaneiventris* (Short, 1969c).

Sicalis flaveola

Saffron Finch

Figure 72

Taxonomy. Polytypic. Its relationships with other congeneric species are unclear.

Ecology. Frequents forest clearings and edges, woodlands, savannas, and open grasslands, flying far from one to another cluster of trees. Highly social, cardueline in habits, but nests in scattered pairs, in crevices of trees (personal observ.). Wanders in flocks when not breeding, and forages for seeds (and possibly insects) even when breeding.

Distribution and variation. Endemic in South America (introduced elsewhere). It is found in northern Colombia across Venezuela to the Guianas, including the Colombian llanos, in western Ecuador and northeastern Peru, and from Maranhão and Ceará to Goiás, Mato Grosso, and eastern Bolivia in the interior, and to Pernambuco and thence S along the coast to Uruguay and northern Buenos Aires, and S inland to Mendoza and La Pampa. Of the four races currently recognized, the distinct *pelzelni* occurs from central Mato Grosso, São Paulo, and Paraná to eastern Bolivia, Mendoza, and Buenos Aires. Intergrading with *brasiliensis* in eastern Mato Grosso and São Paulo, *pelzelni* is very pale, males lack gold in their yellow, and they are very streaked above and below; females virtually lack yellow, are much browner than other races, and they are brown streaked on white below. This race occurs in all of the chaco and extends beyond the chaco slightly to the W, and extensively N, E, and S.

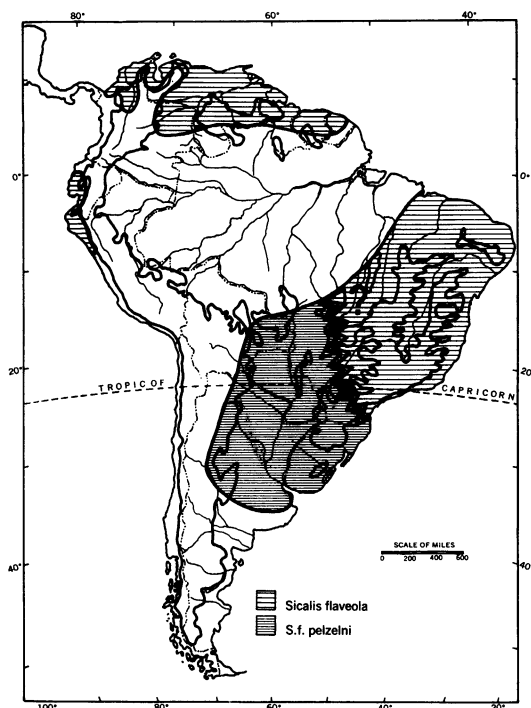


FIG. 72. Range of Saffron Finch (*Sicalis flaveola*). Isolates form distinct races, except that in southeastern isolate two well-marked subspecies meet and intergrade (western *pelzelni* with eastern *brasiliensis*, latter east of zigzag line) as shown, but their intergradation is in need of study in its northern area. Species is distributed in diverse habitats, but avoids highlands and Amazonian forest.

Sicalis luteola

Grassland Yellow-finch

Taxonomy. Polytypic. Relationships not clear.

Ecology. Habits like *flaveola*, but found more often in open country, although it also frequents forest edges and clearings. Wanders when not breeding, and is partly migratory. Very social.

Distribution and variation. Middle and South America. In South America three disjunct and distinct populations occur: the *bogotensis* group in the Andes from Colombia S to southern Peru, and to northern Venezuela, related to the *chrysops* group of Middle America; the *luteola* group in lowland Colombia, northern and southeastern Venezuela, Guyana, French Guiana and

northeastern Brazil S to the lower Amazon Valley; and, *luteiventris* breeding from southeastern Peru, eastern Bolivia, Mato Grosso, Goiás, and Rio de Janeiro S through Paraguay and southern Brazil to Uruguay, Río Negro, Neuquén, and north-central Chile. The latter race is very large, males are pale with no orange-gold, and females are not yellowish but more tan below and browner generally (yellow traces on underparts and on rump only). This subspecies inhabits the entire chaco and extends beyond the chaco slightly W into the lower Andean slopes and extensively N, E, and S.

Lophospingus pusillus
Black-crested Finch

Figure 73

Taxonomy. Monotypic, sympatric with *griseocristatus*, its nearest relative.

Ecology. Lives in chaco woodlands, and (monte) brushlands. Habits little known. Non-migratory.

Distribution. Endemic in south-central South America. Inhabits the chaco from Santa Cruz, Bolivia S through the Paraguayan chaco, Formosa, Chaco, and Córdoba to San Luis and La Rioja, and W to Catamarca, Jujuy, and Tarija. Its range centers in the chaco, and the monte. It inhabits all the chaco except the pantanal (including Mato Grosso) and northern Santa Fe, and thus is found in the drier woodlands of the chaco. Its range extends mainly SW beyond the chaco.

Coryphospingus cucullatus
Red-crested Finch

Figure 74

Taxonomy. Polytypic. Forms a superspecies with eastern and northern South American *pileatus*, which occurs disjunctly in southern Colombia, in northeastern Colombia across northern Venezuela, and from Goiás and Ceará S through Bahía and Minas Gerais to Rio de Janeiro. *Coryphospingus pileatus* is mainly gray rather than reddish, the red being restricted to the crown patch. The two species may prove to be conspecific (Paynter, 1970, p. 211). It is a moot point whether or not they meet during the breeding season in eastern Brazil; their ranges approach closely, but northern *cucullatus* individuals in that region may be migrants.

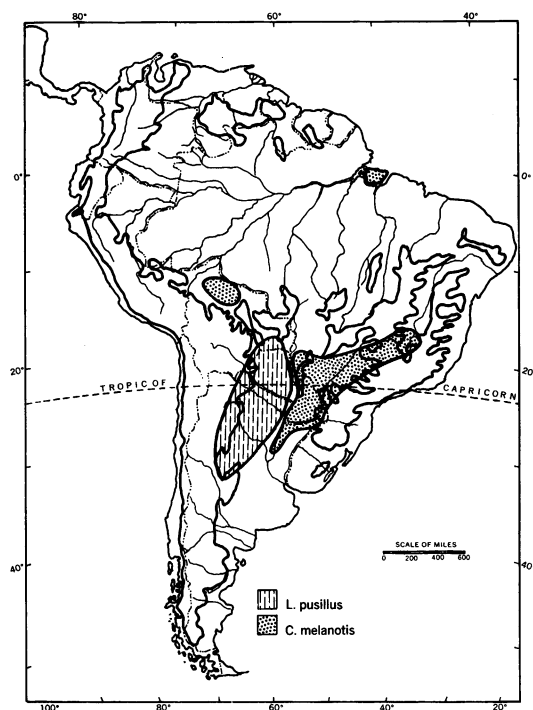


FIG. 73. Range of Black-crested Finch (*Lophospingus pusillus*) and Black-masked Finch (*Coryphospiza melanotis*). Former is species of dry chaco and dry subtropical forest. *Coryphospiza melanotis* occurs in three disjunct populations, the northern (Marajo Island) isolate being racially separable from the others. This species of moist wooded grasslands is restricted to pantanal in the chaco.

Ecology. Found in brushy areas such as undergrowth of forests and woodland edges. Migratory. Insectivorous and granivorous. Territorial.

Distribution and variation. The superspecies is endemic in South America. *Coryphospingus cucullatus* occurs disjunctly from the Guianas to the mouth of the Amazon and eastern Pará, and from central Bolivia, Mato Grosso and São Paulo S to La Rioja, Santa Fe, and Uruguay. The southern populations are migratory, and the northern limits of their ranges are uncertain. *Coryphospingus cucullatus fargoii* is grayer above (males) and less bright red below than races to the E and N. This form occurs in the chaco and S to Santa Fe, Córdoba, and La Rioja, and W to the monte along the Andean slopes N to central Bolivia. It

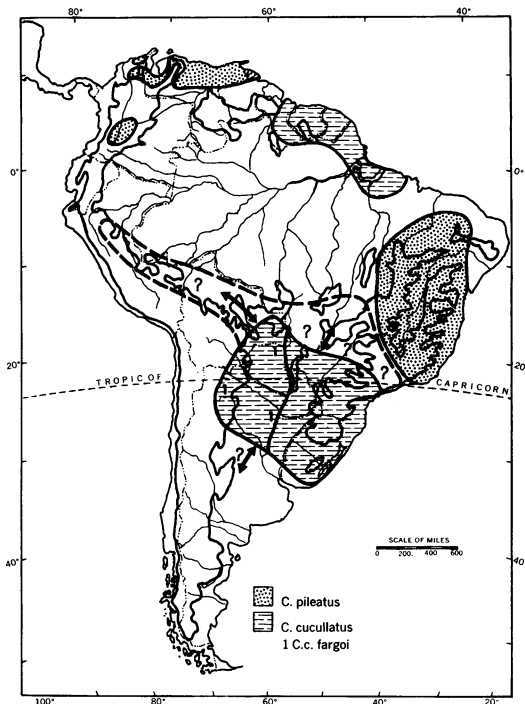


FIG. 74. Range of Red-crested Finch (*Coryphospingus cucullatus*), and its allospecies *C. pileatus*. The more southern populations of *cucullatus* are somewhat migratory (broken line, arrows). Study to determine if this is responsible for their apparent parapatry (eastern Brazil) is needed. Note isolates of both species. Southern *cucullatus* consists of two subspecies that intergrade in eastern chaco; these frequent forest undergrowth and brushland of southeastern Brazilian forest, chaco, dry subtropical forest, and adjacent (ecotonal) areas.

occupies the entire chaco, intergrading in the E with contiguous *C. c. rubescens*.

Arremon flavirostris
Saffron-billed Sparrow
Figure 75

Taxonomy. Polytypic. The genus is weakly characterized, and consists of a single superspecies, comprised of five allospecies. These are: Middle American and northwestern South American (western Colombia, northwestern Ecuador, eastern Ecuador, and northeastern Peru) *aurantiirrostris*; northern Colombian and northwestern

Venezuelan *schlegeli*; *abiellei* of southwestern Ecuador and adjacent Peru; *taciturnus* of eastern Colombia, southern Venezuela, the Guianas, the lower Amazon region, southern Amazonia (southeastern Peru, northern Bolivia, Rondonia, eastern Amazonia), Mato Grosso, Goiás, and Pará and Maranhão E to the eastern corner of Brazil, thence S along the coast to Santa Catarina or possibly Rio Grande do Sul; and *flavirostris* of south-central South America. *Arremon taciturnus* is variable, with a partial, complete, or no pectoral band, a yellow-green back, and a broad central crown stripe. *Arremon flavirostris* is generally like *taciturnus* (which it seems to meet in eastern Brazil without interbreeding), differing consistently only in the yellow base of its upper bill and, usually, larger yellow area on the tomia of the bill; the bill of *taciturnus* is black, or mainly black, and that of *flavirostris* about half black and half yellow. *Arremon aurantiirrostris* generally resembles *taciturnus*, but is greener above with a rusty tint and no yellowish; it has an orange or almost completely orange bill and a broad pectoral band. *Arremon schlegeli* has a black head (no head stripes) and a yellow bill. *Arremon abiellei* is either green or gray above, with a black cap like some forms of *flavirostris*, but the bill is all black and its wings are gray with virtually no yellow or yellow-green. All are allopatric, with contact most likely to occur between *flavirostris* and *taciturnus* in Minas Gerais and São Paulo, but their distribution is not known precisely.

Ecology. *Arremon flavirostris* inhabits low brush and the ground in forests and woodlands. Builds a covered-over nest upon the ground (personal observ.). Nonmigratory. Territorial. Insectivorous and granivorous.

Distribution and variation. *Arremon flavirostris* (and three of the other four species in this superspecies) is endemic in South America. It is found from western Minas Gerais and Bahía SW to western São Paulo and Mato Grosso to easternmost Bolivia, and S through central and eastern Paraguay to eastern Chaco Province, Misiones, and western Paraná; in the W from central Bolivia S to Tucumán and Catamarca. It is doubtful whether eastern and western populations meet in the northern Paraguayan chaco or in Santa Cruz, Bolivia, but there is a gap from the south-central chaco of Paraguay S, including the central Argentinian

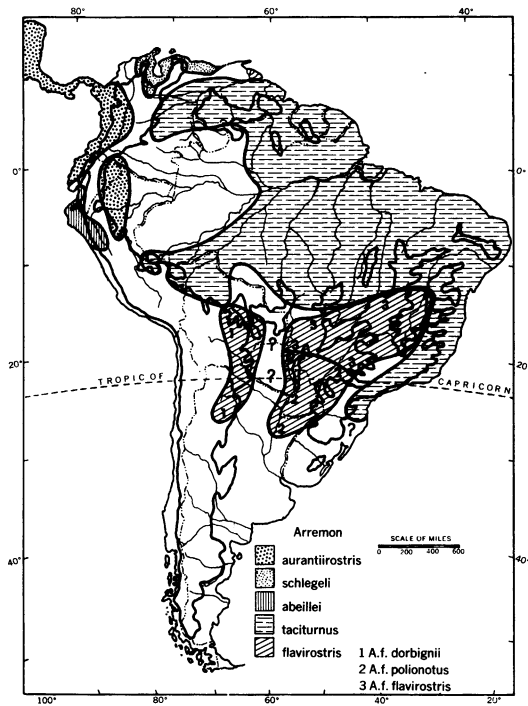


FIG. 75. Range of five allospecies of super-species *Arremon taciturnus*, including Saffron-billed Sparrow, *A. flavirostris*, of chaco region. Note allopatric and parapatric distributions of allospecies. *Arremon flavirostris* is parapatric with adjacent *taciturnus*; their interactions are in need of study. Dry central chaco separates (possibly there is contact) two eastern races of *flavirostris* from western *A. f. dorbignii*. *Arremon flavirostris* is a species of dry subtropical forest, wetter parts of chaco, southeastern campo cerrado, and fringe of southeastern Brazilian forest.

tine chaco. The western population comprises *A. f. dorbignii*, a green-backed subspecies which may reach the western fringes of the chaco along its entire length. In the E, gray-backed *A. f. polionotus* occurs from southwestern Mato Grosso and the pantanal region of the chaco and eastern chaco woodland from northern Paraguay to northern Chaco, Argentina, and from there E to Misiones, western Paraná, and southeastern Mato Grosso. *Arremon flavirostris devillii* inhabits the northernmost chaco of eastern Santa Cruz, Bolivia, and adjacent Mato Grosso, and the area E to São Paulo and Goiás; it is gray-backed like

polionotus (note that the northeastern race *flavirostris* is green-backed, like *dorbignii*), but has more green in the wings than does the latter.

Ammodramus humeralis
Grassland Sparrow
Figure 76

Taxonomy. Polytypic. Forms a superspecies with *A. aurifrons* of western Amazonia and the Amazon Valley (eastern Colombia and southwestern Venezuela S through eastern Ecuador and eastern Peru to eastern Bolivia, in western Amazonia, and E through the Amazon Valley to its mouth). The latter overlaps with *humeralis* in north-central Bolivia, parts of eastern Colombia and southwestern Venezuela, and in a few places

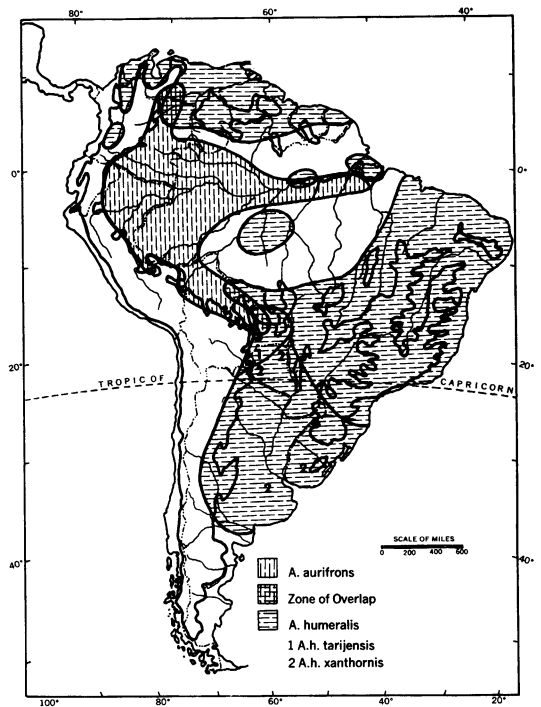


FIG. 76. Range of Grassland Sparrow (*Ammodramus humeralis*) and its allospecies *A. aurifrons*. Latter basically is western Amazonian. Note various isolates of *humeralis* and its areas of overlap with *aurifrons*. *Ammodramus humeralis* occurs in grasslands wherever they are found, whether as patches in wet forest, or woodlands, or as extensive savannas and grasslands.

in the lower Amazon Valley, but generally the two replace each other. *Ammodramus humeralis* is darker above, with more shades of brown giving a strongly scalloped effect, has a stubbier bill, and its facial yellow is restricted to the anterior superciliary stripes. *Ammodramus aurifrons* is paler, more simply patterned above, with a longer, narrower bill and yellow on the superciliary stripes and around the orbits. They seem closely related to *A. savannarum* (Mayr and Short, 1970) and have been merged in *Ammodramus* by Paynter (1970).

Ecology. *Ammodramus humeralis* is a grassland and savanna species which is able to utilize somewhat overgrown, shrubby grasslands. It occurs in clearings in woodlands and forested regions. Nonmigratory.

Distribution and variation. The superspecies is endemic in South America. Isolates occur in southern Colombia, from northern Colombia across Venezuela to the Guianas and S to northeastern Colombia (Ilanos) and northernmost Brazil, about the mouth of the Amazon, in eastern Amazonas, and from Maranhão, Goiás, Mato Grosso, and north-central Bolivia S through all of eastern and southern Brazil, Paraguay, Uruguay, and the lowlands and Andean slopes of Argentina as far S as Río Negro. *Ammodramus humeralis xanthornus*, the southern race, occurring S of Bolivia, Mato Grosso, and Paraná, is characterized by its large size. *Ammodramus humeralis tarijensis*, doubtfully distinct from *xanthornus* (slightly browner and slightly larger), occurs in Bolivia and possibly adjacent Paraguay. Thus, the species occupies all of the chaco in suitable habitat, with *tarijensis* occurring in the northern (Bolivian chaco) and northwestern (southern Bolivia, Paraguayan border) fringes of the chaco, and *xanthornus* occurring S from the northern chaco (pantanal of Mato Grosso) throughout the chaco and beyond to the E, S, and W.

Aimophila strigiceps
Stripe-capped Sparrow
Figure 41

Taxonomy. Polytypic. Seems closely related to *Aimophila (Rhynchospiza) stolzmanni* of Peru, and *A. sumichrasti* of Middle America. The disjunct occurrence of these xeric-adapted spar-

rows across the tropics is interesting and parallels the case of *Picooides mixtus-lignarius-scalaris*.

Ecology. In brushland, found neither in woodlands nor in grassland, but in chaco scrub within the pampas-chaco ecotone, and in monte W of the chaco. Forages in bushes and grasses and on ground for insects and seeds. Partly migratory.

Distribution and variation. Endemic in south-central South America. Disjunct populations occur in Jujuy and Salta S to Tucumán, and from Santiago del Estero to Córdoba, Chaco, Santa Fe, and Entre Ríos. The western *A. s. dabbenei* is considerably smaller, less rufous above, more tan below, and with less black on the bill and lores than eastern *A. s. strigiceps*. The latter occurs in the southeastern chaco from Chaco and Santiago del Estero S, beyond the chaco to Córdoba, southern Santa Fe, and Entre Ríos.

Junco capensis
Rufous-collared Sparrow

Taxonomy. Highly polytypic. Not especially close to other species of its genus, but is the tropical (and temperate South American) representative of *Junco* (it is rather more subtropical and temperate than tropical in its distribution). *Zonotrichia* is merged in *Junco* for reasons I have presented in detail elsewhere (in Mayr and Short, 1970, pp. 85-86); merger of other genera with *Zonotrichia* without including *Junco* creates a polyphyletic genus, because *Junco hyemalis* and *phaeonotus* are near relatives of *J. (Zonotrichia) albicollis* and its relatives.

Ecology. Edge and undergrowth species in forests, woodlands, savannas, and bushy areas in grasslands. An abundant bird, common in cultivated areas and gardens in villages and even cities. Nests on the ground or in bushes and trees (up to several meters above ground in areas subjected to flooding). Forages for insects and seeds. Partly migratory. Territorial.

Distribution and variation. Found in Middle and South America and the West Indies. In South America it is found in the highlands and slopes of mountains from northern Venezuela and northern Colombia S along the Andes (coastally in Peru and S from there) to Bolivia, and throughout lowlands and highlands from Bolivia and

Mato Grosso S to Tierra del Fuego; from Bolivia and the Argentine Andes E across Argentina, Paraguay, Uruguay and southern Brazil N along the coast to Pernambuco and in the highlands and interior plateaus and lowlands N to Goiás and Maranhão; in eastern Pará and about the mouth of the Amazon; and N of the lower Amazon through northeastern Brazil and the Guianan highlands to the Guianan lowlands, and southeastern Venezuela. The many races vary in their degree of differentiation. *Junco capensis hypoleuca* (including "mellea") is a pale race, showing little rufous dorsally and on the wings and hind-neck. It occurs from central Bolivia and western Paraguay S through the lowlands and eastern Andean slopes to Mendoza, La Pampa and Buenos Aires; it occurs E to the Uruguay River, eastern Corrientes, southeastern Paraguay, the Paraguay River and Mato Grosso. Thus, it occupies the entire chaco, and extends mainly S, and to some extent NW and W of it.

Coryphasiza melanotis

Black-masked Finch

Figure 73

Taxonomy. Polytypic. Probably related to *Emberizoides*.

Ecology. In savannas, favoring tall grassy areas. Little known.

Distribution and variation. Endemic in South America. Disjunct populations occur on Marajo Island at the mouth of the Amazon River, in northern Bolivia, and from southwestern Mato Grosso E to São Paulo and Minas Gerais, and S to eastern Paraguay, Misiones, Corrientes, eastern Chaco Province, and northern Santa Fe. The nominate race occurs in Bolivia and S from Mato Grosso and Minas Gerais; it is larger and more red-brown than *marajoura* of Marajo Island. This form inhabits the pantanal of the chaco in Mato Grosso, eastern Chaco, northeastern Santa Fe, and probably eastern Formosa and the Paraguay River region of the Paraguayan chaco.

Emberizoides herbicola

Wedge-tailed Grass-finch

Taxonomy. Polytypic. An appraisal of the grass-finches led to the description of a sibling species, *E. ypiranganus*, broadly sympatric with

herbicola (Eisenmann and Short, MS; the late W. Partridge first distinguished the two species). Features of these species stimulated the investigation of variation in *herbicola*, and Eisenmann and Short concluded that the very large, dark, differently proportioned *E. h. duidae* of Duida Mountain, Venezuela, also is specifically distinct from *herbicola*. Its isolation on the table top of that steep-sided mountain, with *E. herbicola sphenurus* present at the base, merits its status as an allospecies in a superspecies with *herbicola*.

Ecology. Inhabits tall grass, often with bushes interspersed as at the edges of forest. Insectivorous and granivorous. Territorial. Non-migratory.

Distribution and variation. Southern Middle America and South America. In the latter region it is found from western Colombia across northern Colombia, Venezuela, and eastern Colombia, the Guianas, Amapá, Brazil, and from the mouth of the Amazon to northern Maranhão; and from Pernambuco, Goiás, and Minas Gerais W to northern Bolivia and S through central Paraguay and all of southern Brazil to northern Santa Fe, Corrientes, and Rio Grande do Sul. The southern range S from Bolivia and Pernambuco is occupied by *E. h. herbicola*, the largest of the subspecies; it is pale in color and buffier below than northern races. This subspecies is found in the pantanal and openings in the eastern chaco woodland throughout the eastern chaco, and from there E and N.

Emberizoides ypiranganus

Dark-cheeked Grass-finch

Taxonomy. Monotypic (possibly clinally larger to N). Sibling species of sympatric *E. herbicola*, which see.

Ecology. Favors wet grassy areas about woodlands and forests. Little known, but probably nonmigratory. Territorial.

Distribution. Endemic in south-central South America from northern Paraguay (E of the Paraguay River) and São Paulo S to northern Santa Fe, Corrientes and Rio Grande do Sul (known so far from eastern Paraguay, São Paulo, Santa Catarina, Rio Grande do Sul, Misiones, Corrientes, and northern Santa Fe). Thus far it is known to occur in the chaco only in the Mocoví

region of Santa Fe, but it is likely to occur throughout the pantanal region. Its range extends E from the eastern chaco.

Embernagra platensis
Great Pampa-finch
Figure 77

Taxonomy. Polytypic. Forms a superspecies with the rare *E. longicauda* of Bahía. The latter has a long "wedge" tail, and a buffy throat and breast, but otherwise closely resembles *platensis*. Skeletons of *platensis* show great similarity to those of *Emberizoides herbicola* and *E. ypiranganus*, and juvenile specimens of all three species are extremely similar; I consider it very likely that they are congeneric and close relatives.

Ecology. Frequents grassy areas, both dry

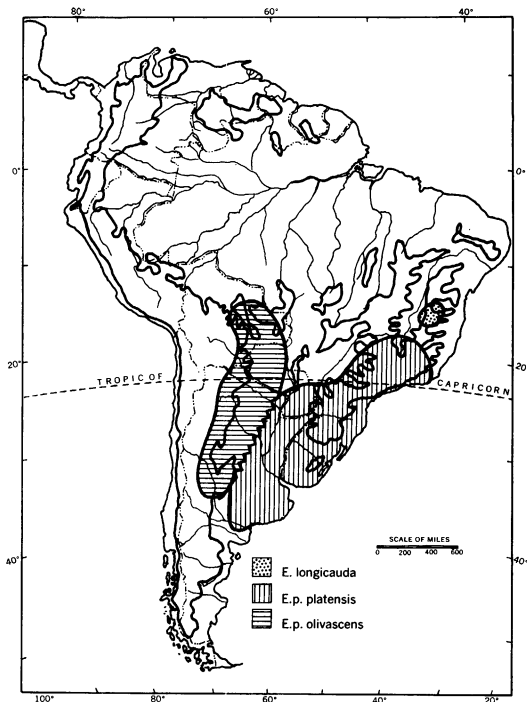


FIG. 77. Range of Great Pampa-Finch (*Embernagra platensis*) and its allospecies *E. longicauda*. Latter is rare and little known. Two well-marked races of *platensis* intergrade in east-central chaco. Distribution pampas-southeastern Brazilian forest, chaco, chaco scrub, and dry subtropical forest.

and wet, including very small grassy, bushy clearings in forests and woodland edges and pampas. Generally more common than either *Emberizoides herbicola* or *E. ypiranganus*. Nonmigratory. Territorial.

Distribution and variation. Endemic in South America (as is the superspecies). Found in east-central and eastern Bolivia, western south-central and eastern Paraguay, São Paulo, Minas Gerais, and Rio de Janeiro S to Mendoza, La Pampa, and Río Negro. Well-marked races occur in the W and E. The eastern *platensis* ranges from eastern Formosa, Santa Fe, and Córdoba E to La Pampa, Buenos Aires, Uruguay, and coastal Brazil N to Rio de Janeiro. Western *olivascens* occupies the region from central Bolivia S through the western Paraguayan chaco, the lower slopes of the Andes, and the western Argentine chaco to Mendoza and San Luis. The latter race is much larger, it lacks the dorsal streaks of *platensis*, and its bill is more strongly curved. The chaco is inhabited partly by *platensis* in the pantanal and eastern chaco woodland from central Paraguay S to Santa Fe; it extends NE, E, and SE from there. *Embernagra platensis olivascens* occurs throughout the central and western chaco from Santa Cruz, Bolivia to Santiago del Estero, and beyond it to the NW, the W, and the S. Only the northern pantanal of Mato Grosso and northern Paraguay lack this finch.

Donacospiza albifrons
Long-tailed Reed-finch
Figure 78

Taxonomy. Monotypic. Related to *Poospiza*.

Ecology. Edge species of forests, woodlands, and brushy areas of pampas. Territorial. Non-migratory.

Distribution. Endemic in east-central South America. Found from the eastern chaco (eastern Paraguayan chaco, eastern Formosa, Chaco, and Santa Fe) E to Minas Gerais, Rio de Janeiro, coastal southern Brazil, Uruguay, and northern Buenos Aires. It is lacking in the central, western, and northern chaco.

Poospiza torquata
Ringed Warbling-finch

Taxonomy. Polytypic. Forms a superspecies with southwestern Ecuadorian and north-

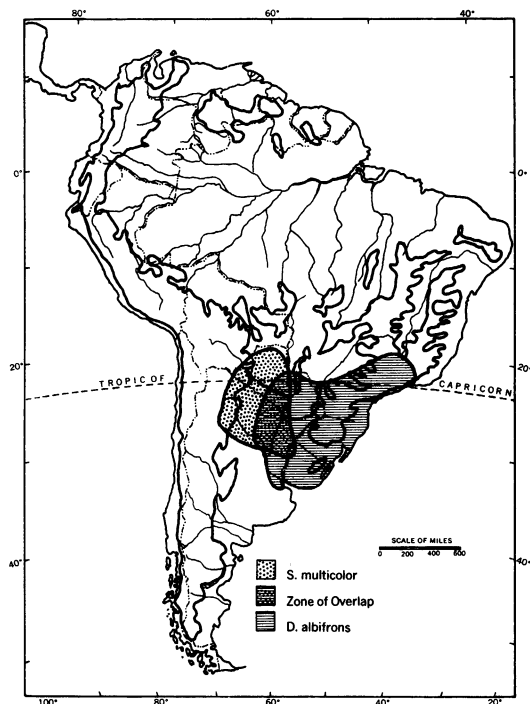


FIG. 78. Range of Long-tailed Reed-Finch (*Donacospiza albifrons*) and of Many-colored Chaco-Finch (*Saltatricula multicolor*). These monotypic species are not closely related. *Donacospiza albifrons* is a southeastern Brazilian forest and pampas finch that extends well into eastern chaco. *Saltatricula multicolor* largely occurs in chaco, barely extending beyond it to east and west.

western Peruvian *hispaniolensis*, with which it may be conspecific (Meyer de Schauensee, 1966). They are similar in pattern: both have a black breast patch, gray back, similar black and white head pattern, white in the wings, and white in the tail. *Poospiza torquata* is smaller billed, without brown traces in the back, with a more complete breast patch (not restricted at the sides by gray), and with more white in the wings and tail than *hispaniolensis*. *Poospiza torquata* also is less dimorphic sexually, females resembling males but with duller colors; in *hispaniolensis* females are markedly different, being brown, without a breast patch or with only traces of it, and with a pale rather than a black bill like that of the male. The superspecies may be related to the

erythrophrys group as well as to *P. cinerea-melanoleuca*.

Ecology. Grassland and brushland finch, usually found where at least some bushes are present. Partly migratory. Semi-social when not breeding.

Distribution and variation. The superspecies is endemic in South America. *Poospiza torquata* occurs from central-western Bolivia through the eastern edge of the highlands and adjacent slopes to the Andean slopes of Argentina S to Mendoza, and E across the lowlands of Argentina to the lower Paraguay River, Entre Ríos, and coastal Buenos Aires. The highland Bolivian race *torquata*, of arid upland valleys, is larger than lowland Bolivian (Tarija) and Argentine *pectoralis*, and its bill is notably larger than in the latter. *Poospiza torquata pectoralis* inhabits the southern chaco from Salta and Formosa to Tucumán and Santa Fe and beyond to the S and W (into sub-Andean monte). This form migrates into the northern chaco in the fall.

Poospiza melanoleuca

Black-capped Warbling-finch

Taxonomy. Monotypic. Forms a superspecies with *P. cinerea*, with which it is merged by Paynter (1970; he uses *cinerea* as the name for the species, although *melanoleuca* has priority). *Poospiza cinerea* occurs in eastern and central Mato Grosso, Goiás, Minas Gerais, and northern São Paulo. It is gray above and white below, like *melanoleuca*, but it is slightly larger, with a longer, thinner, and paler bill, and it has no sign of the black cap of *melanoleuca*. They appear not to meet, although their ranges approach each other in Mato Grosso.

Ecology. Edge species, requiring bushes and low trees adjacent to grassland, hence found in open chaco woods, savannas, and the northwestern pampas region, as well as monte and chaco scrub. Apparently it is not migratory.

Distribution. The superspecies is endemic in central South America. *Poospiza melanoleuca* occurs from northern Bolivia S along the Andean slopes and through the chaco to southeastern Paraguay, Corrientes, western Uruguay, Buenos Aires, and La Rioja. It occupies the entire chaco, including southwestern Mato Grosso, and ex-

tends beyond the chaco mainly S, SE, and NW, and also slightly to the W.

Poospiza nigrorufa
Black and Rufous Warbling-finch

Taxonomy. Strongly polytypic. Probably related closely to *erythrophrys*, and possibly *ornata*.

Ecology. Found in grasslands, especially where some small bushes and trees are present. Nonmigratory. Territorial.

Distribution and variation. Endemic in south-central South America. Found from the Andean slopes of northern Bolivia S along the Andes to Catamarca, and in lowlands of western Córdoba (*whitii* group), and central Paraguay S through eastern Argentina (W to eastern Formosa, and Santa Fe, and E to Misiones) to Rio Grande do Sul, all of Uruguay, Buenos Aires, and northern Río Negro (*P. n. nigrorufa*). The western *whitii* group (including widespread *whitii* and *wagneri*, known from a single locality in La Paz) is strongly divergent from allopatric *nigrorufa*, being much smaller, grayer dorsally, chestnut rather than cinnamon below, and with more white in the tail. *Poospiza nigrorufa whitii* may reach the chaco in the W, especially the SW (Santiago del Estero). *Poospiza nigrorufa nigrorufa* inhabits the southeastern chaco from central Paraguay to Santa Fe (in pantanal, mainly), and it extends E and S of the chaco.

Saltatricula multicolor
Many-colored Chaco-finch
Figure 78

Taxonomy. Monotypic species and genus. Relationships uncertain but *Poospiza*-like in habits and appearance.

Ecology. A woodland edge species, strongly associated with chaco woodland. Nonmigratory.

Distribution. Endemic in central South America, from southern Bolivia and western Paraguay S along the edge of the Andes and in the lowlands to La Rioja, Córdoba, Entre Ríos, Corrientes, and western Uruguay. It inhabits all the chaco except the extreme N (Bolivia, northernmost Paraguay, Mato Grosso) and extends slightly W, S, and SE from there.

FAMILY CARDUELIDAE

Carduelis (Spinus) magellanica
Hooded Siskin

Figure 79

Taxonomy. Polytypic. Included provisionally in the same superspecies are Middle American *notata*, Patagonian and Chilean *barbata*, and west Ecuadorian *siemiradzkii*. I consider *olivaceus* and *santaecrucis* as races of *magellanica*. *Carduelis notata* resembles *C. magellanica* except for its usually longer, thinner bill, and sexual monomorphism in some races. *Carduelis siemiradzkii* resembles both of these species (both sexes), but is smaller in size and more golden yellow; the

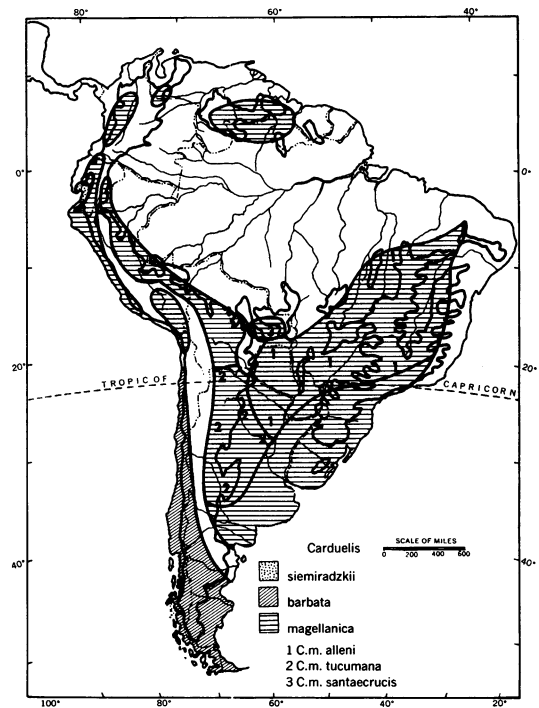


FIG. 79. Range of Hooded Siskin (*Carduelis magellanica*), and two of its allospecies, Fuegian and Chilean *C. barbata*, and xeric Ecuadorian *C. siemiradzkii*. *Carduelis magellanica* occupies xeric to wet forested and grassland areas, both in lowlands and mountains, but it avoids tropical forests. Note isolates of *magellanica*. Little is known of interactions, including intergradation of various distinctive subspecies of *magellanica*, including those chaco-inhabiting subspecies indicated.

backs of males are olive-yellow, not yellow-green, and they lack the streaking prevalent in the other two species. *Carduelis barbata* is not black-hooded like the other species (the hood appears to have been reduced to a throat patch and crown patch), and it is larger, but its range complements that of *magellanica* and it is otherwise similar in pattern.

Ecology. Typically cardueline, occurring in small to large flocks much of the year. Requires trees for nesting, but is found in all manner of habitats, including village gardens. Wanders when not breeding.

Distribution and variation. Three of the four allospecies are endemic in South America, *notata* being Middle American. *Carduelis magellanica* occurs disjunctly in the highlands of southeastern Venezuela and Guyana, and adjacent Brazil, in southwestern Venezuela and adjacent Colombia, in central Andean Colombia, from eastern Ecuador to southeastern Peru along the eastern slope of the Andes, in the southern Andean highlands of Peru, in the Andean highlands from southern Colombia to north-central Peru, along the Pacific slope from southwestern Ecuador to southern Peru, in the Andes of northern Chile and adjacent Bolivia, and in central Bolivia and from there E across eastern Bolivia and Mato Grosso to Piauí, and S to coastal Brazil at Rio de Janeiro, thence S to Uruguay, Buenos Aires, and northern Río Negro, and W to the upper slopes and valleys of the Andes. The large, dorsally very black marked *santaecrucis* occurs in Santa Cruz, eastern Bolivia; it is often treated as a separate species as is *olivacea*, a small, bright yellowish but olive-sided and olive-backed form of the eastern Andean slopes from eastern Ecuador to north-central Bolivia. Of the many races *C. m. alleni* is a lowland form of Paraguay (except the SE), Formosa, and Chaco, Argentina, and from there NE (northern São Paulo, to Piauí). Males of this form are very olive (little yellow) above, with few dark spots. *Carduelis magellanica tucumana*, a large (including bill) race with very pale coloration and reduction of the cap and throat portion of the hood (a tendency extended in adjacent *C. barbata*), occurs from Jujuy, Santiago del Estero, and Santa Fe S to Mendoza, San Juan, and Córdoba. The latter race occupies the southern edge and southwestern corner of the

chaco, extending S and W. *Carduelis magellanica alleni* inhabits all of the northern and much of the eastern chaco, and extends NE from there.

SYSTEMATIC SUMMARY

The chaco avifauna numbers 409 species, including 23 species barely reaching its borders. Of these, 218 are nonpasserines, 100 (including 52 tyrant flycatchers) are suboscines, 20 represent Old World oscine groups, and 71 are nine-primaried oscines (including cardueline finches). Relative proportions of these species may be placed in perspective by comparison with the similarly treated (Mayr and Short, 1970), although 50 percent larger, North American avifauna, totaling 607 species. Nonpasserine species comprise about the same proportion (53% of chaco birds, 55% of North American species) of both avifaunas. Suboscines are South American in origin, hence are much more conspicuous an element (24% of chaco, 6% of North American avifauna) of the chaco avifauna than of the North American avifauna. Old World oscines diminish southwardly in the New World; they form 14 percent of the North American avifauna, and 5 percent of the chaco avifauna (their numbers remain that high because of New World tropical radiation among jays and gnatcatchers, and because mimids and troglodytids, although of Old World ancestry, are New World groups with substantial South American elements). Nine-primaried oscines, basically a New World assemblage but thought to have originated in tropical North America (see, e.g., Mayr, 1946), are somewhat less numerous in the chaco than in North America (17% of chaco birds, 25% of North American birds in this group). Several elements of the nine-primaried oscines (e.g., tanagers, blackbirds, emberizine and cardinaline finches) have extensive South American radiations, and account for most of the chaco species in this category.

Polytypy among chaco species involves 65 percent (141 of 218) of its nonpasserine birds, and 71 percent (135 of 191) of its passerine species. These proportions are a trifle higher, but not substantially so, than the 63 and 66 percent, respectively, for North American species in these categories. Only a bit more polytypy is evident in

passerine than in nonpasserine birds of both regions. One might expect lesser proportions of chaco species showing polytypy because South American birds are less well-known than those of North America, and because the latter may be somewhat oversplit taxonomically. However, these possible factors are balanced by uneven treatment of diverse South American birds, some groups having been split (e.g., some tinamous) overly much and others (e.g., tyrant flycatchers), studied less intensively, having insufficient definition of subspecies.

Approximately one-third of the chaco species are allospecies within superspecies. Passerine superspecies number 68 out of 191 zoogeographical species (which include superspecies plus species not within superspecies, and exclude allospecies of superspecies), or 37 percent, and

nonpasserine superspecies number 69 of 213 zoogeographical species, or 32 percent. About one-quarter of North American zoogeographical species are superspecies (28% of nonpasserine and 21% of passerine species; Mayr and Short, 1970, pp. 100-101). The North American proportion of superspecies appears to be low in comparison with the chaco, and probably with continental areas in and near the tropics generally. Hall and Moreau (1970) found that about 50 percent of African passerine species (not zoogeographic species, thus giving a higher percentage than would be obtained using the latter) are members of superspecies. Other comparative data are needed, particularly for tropical South America and Asia.

Some other aspects of the zoogeographic information presented above will be treated in the following section.

THE DISTRIBUTION OF CHACO BIRDS

Avian species often are distributed widely, and birds occurring in the chaco tend to range far beyond that region. Barriers to their distribution are nonexistent, or ineffective, accounting for the low endemism of the chaco avifauna, and for the fact that chaco species occur in many parts of South America, and beyond. I shall examine the patterns of distribution, particularly the broad ranges of some species, the endemism of the chaco, range disjunctions, and zones of intergradation and secondary contacts involving chaco birds so that these aspects of distribution may shed light on the origins of the chaco avifauna.

THE OCCURRENCE OF CHACO BIRDS OUTSIDE OF SOUTH AMERICA

The majority (252 of 409) of chaco birds are endemic in South America. Of the 157 non-endemic species (comprising 38.8% of the total 409 species), 155 reach Middle America (38%), 51 attain North America (12%), and 11 species (3%, all nonpasserine) extend into the Old World.

The consideration of avian distribution beyond the limits of South America must be prefaced by mention of the barriers limiting distribution to that continent, namely the great ex-

panses of ocean to the east (Atlantic), south (Antarctic Ocean and inhospitable Antarctica), and west (Pacific). The distribution of species to the north is less affected adversely, but the relative accessibility of habitats, related to the small mass of continuous land to the north, are crucial in limiting avian distribution. South America is very broad just south of the equator, but from the equator northward the land area of the Western Hemisphere is constricted, and reduced finally to the narrow Panamanian land mass connecting South America with Middle America. To the north, beyond the tropics, the land area expands abruptly into North America. The present small extent of land area in Middle America and the restriction of its various habitats by orogenic topography doubtless impedes the extension northward of many avian species. Likewise, past changes in habitat, orogeny, and emergence of the Panamanian land bridge (Haffer, 1970b, p. 618) have diversely affected extension of ranges of many species, adding to the filtering effect posed by the character and size of the Middle American land mass. South of the equator, on the contrary, the vast land mass gradually tapers and is restricted only far to the south. Birds have now, and must have had in the recent past, easy access to suitable habitats south of the equator.

Of course, past climatic shifts and correlated habitat modifications placed limitations on their distribution.

Chaco Birds Outside South America and Their North-South Limits

Those chaco species extending well into Middle America (i.e., beyond Panama) or even beyond that region to North America were analyzed to establish their northern and southern distributional limits. As expected, these chaco species generally were found to extend farther south than north of the equator. Of monotypic and polytypic species lacking racial differences between the northern and southern extremes of their ranges, none extends farther north than south, seven have essentially the same northern and southern limits (that is, the northern and southern limits fall within 3° of latitude of each other), and 17 have southern limits exceeding (by more than 3° latitude) their northern limits. Most of the species involved are tropical or tropical-warm temperate in distribution, but a few extend into cool temperate areas. Among the species with northern and southern limits essentially the same, *Egretta alba* (to latitude 44° N and 46° S) and *Plegadis chihi* (latitude 43° N and 41° S; fig. 18) extend beyond latitude 40° N, and latitude 40° S. Of those 17 species extending farther south than north, only *Nycticorax nycticorax* (to latitude 55° S and to 50° N) extends beyond 40° N or S, and only *Platalea ajaja* (to latitude 30° N), *Dendrocygna viduata* (to 10° N), *Oxyura dominica* (to 26° N), *Charadrius collaris* (to 24° N), and *Tachyphonus rufus* (to 12° N) occur 35° or more (to 38°) south of the equator. The seven species with northern and southern limits approximately the same and the 17 species with a greater extent southwardly include only one passerine species, *Tachyphonus rufus* (fig. 62).

Fourteen polytypic chaco species reaching beyond Panama to the north occur farther north than south. Different races are involved at their range extremes. In four cases (*Falco sparverius*, *Gallinago gallinago*, *Bubo virginianus*, and *Asio flammeus*) the species reach southern Tierra del Fuego (latitude 55° S), hence their greater northward extent (latitude 64° to 71° N) may reflect simply the unavailability of land farther south than latitude 55° S. Only three of the 14 situ-

ations involve passerine birds, namely *Stelgidopteryx ruficollis* (latitude 55° N and 35° S), *Vireo olivaceus* (latitude 61° N and 35° S), and *Parula americana* (latitude 55° N and 35° S).

Although different races are involved at the northern and southern extremes of their ranges, 16 polytypic chaco birds extend approximately as far south as north. *Egretta thula* (latitude 42° N and 39° S), *Cathartes aura* (latitude 54° N and 55° S), *Athene cunicularia* (latitude 54° N and 54° S), and *Troglodytes aedon* (latitude 55° N and 55° S) reach the cool temperate areas of both North and South America. Four of the 16 species are passerine, including *Troglodytes aedon* and *Thamnophilus doliatus* (latitude 23° N and 26° S), *Myiarchus tyrannulus* (latitude 36° N and 34° S), and *Piranga flava* (latitude 36° N and 35° S).

Contrasting with the 14 (or 10, see above) polytypic species showing a greater range extent to the north, and the 16 species extending approximately the same distance north and south of the equator are 76 polytypic species which extend farther south than north. Of these species 47 represent nonpasserine birds and 29 are passerine species. Six species overlap, meet, or closely approach allospecies belonging to their superspecies at their northern limit, and this may account for their restricted northern distribution. These species are *Phalacrocorax olivaceus*, *Accipiter bicolor*, *Ceryle torquata*, *Contopus cinereus* (fig. 47), *Camptostoma imberbe*, and *Progne chalybea* (fig. 54) (*Ictinea plumbea*, one of the monotypic species with a greater southern than northern distribution also closely approaches its northern allospecies *mississippiensis*, and that may be a factor limiting its range northwardly). A number of these southerly inclined species reach cool temperate South America, but fail to do so in North America. These include *Podiceps dominicus* (latitude 55° S and 25° N), *Phalacrocorax auritus* (latitude 55° S and 30° N), *Accipiter bicolor* (latitude 55° S and 23° N), *Parabuteo unicinctus* (latitude 40° S and 33° N), *Polyborus plancus* (latitude 55° S and 33° N), *Falco femoralis* (latitude 55° S and 32° N), *Ceryle torquata* (latitude 55° S and 24° N), *Pyrocephalus rubinus* (latitude 41° S and 37° N), *Tyrannus savanna* (latitude 41° S and 19° N), *Tyrannus melancholicus* (latitude 40° S and 32° N), and *Junco capensis* (latitude 55° S and 17° N). Several of

these species (noted above, and also including *Junco capensis* and perhaps the species of *Tyrannus*) meet or approach very closely related species to the north, and this may restrict their northward distribution. However, *Parabuteo unicinctus*, *Polyborus plancus*, *Falco femoralis*, and *Pyrocephalus rubinus* have no near relatives in the north, and differences between the northern and southern races of these species and probably other factors must account for the north-south differences in distribution. *Tyto alba* and *Cistothorus platensis* range to Tierra del Fuego (latitude 55° S), but they extend northward no farther than latitude 50° N. Many species with more extensive southern ranges reach temperate South America, but do not occupy northern Middle America. Some, perhaps most, of these may be recent invaders of Middle America from South America, and they may be extending their ranges actively at present. Unfavorable habitat or other factors doubtless account for the greater southward distribution of species which reach temperate southern South America (latitude 35° S), and which extend north beyond the Isthmus of Tehuantepec in Mexico, yet fail to reach (or barely reach) the border of the United States of America (latitude 27° to 28° N). Among these species are *Rostrhamus sociabilis*, *Buteo brachyurus*, *Aramides cajanea*, *Poliolimnas flaviventer*, *Leptotila verreauxi*, *Chloroceryle amazona*, *Myiodynastes maculatus*, *Pitangus sulphuratus*, *Cyclarhis gujanensis*, *Saltator coerulescens* (fig. 65), and *Volatinia jacarina*.

When we examine the chaco species represented in Middle and North America by other allospecies of their superspecies, no numerical disparity is evident between superspecies in which the northern allospecies occurs farther from the equator, and those in which the southern allospecies extends farther from the equator. Fifteen superspecies have northern allospecies extending farther from the equator than their southern allospecies. Two cases (*Fulica [atra] americana-leucoptera*, fig. 23, and *Ceryle [alcyon] alcyon-torquata*) involve northern species reaching beyond latitude 60° N, and their southern allospecies reaching Tierra del Fuego (latitude 55° S), beyond which they of course cannot range. Four of the instances involve passerine superspecies. In three of the superspecies three allospecies occur and are involved in the

northern and southern range limits. *Dryocopus [pileatus]* includes the northern allospecies *pileatus*, reaching latitude 61° N, and two southern allospecies reaching (fig. 37) latitude 30° S (*lineatus*) and latitude 31° S (*schulzi*). Likewise, *Progne [subis] subis* occurs north as far as latitude 56° N, whereas in South America *P. [subis] chalybea* reaches latitude 35° S, and *P. [subis] modesta* ranges to latitude 44° S. A reverse situation involves (fig. 47) *Contopus [virens] cinereus*, which reaches latitude 27° S, and its northern allospecies *virens* and *sordidulus*, which occur north respectively to latitude 58° N and 61° N. Two cases involve species ranging from North America to South America, but having a Nearctic allospecies that occurs farther north. These are: *Myiarchus [crinitus] tyrannulus* ranging from latitude 36° N to 34° S, with Nearctic allospecies *crinitus* occurring to latitude 50° N; and *Piranga [rubra] flava* distributed from latitude 36° N to 35° S, with Nearctic allospecies *rubra* ranging to latitude 40° N. Although forest species which occur in both North and South America may be limited southerly by lack of woodlands in the gap from central Argentina to southwestern Argentina and Chile, it is difficult to understand why such southern allospecies as *Ardea [cinerea] cocoi* (latitude 44° S, versus 58° N for Nearctic *cinerea*), *Zenaida [macroura] auriculata* (latitude 42° S versus 55° N for Nearctic and Middle American *macroura*), and *Cypseloides [niger] rothschildi* (latitude 30° S versus 55° N for Middle and North American *niger*) do not extend farther south.

In only five instances do the northern and southern extremes of the ranges of allospecies closely approximate (within 3° latitude) each other. These involve *Crypturellus [undulatus] undulatus* (latitude 27° S) (fig. 12) and *cinna-momea* (latitude 24° N), *Accipiter [bicolor] bicolor* (latitude 55° S) and *cooperii* (latitude 53° N), *Campephilus [melanoleucos] melanoleucos* (latitude 28° S) and *guatemalensis* (latitude 27° N), *Camptostoma [obsoletum] imberbe* (latitude 31° S) and *obsoletum* (latitude 32° N), and *Pheucticus [chrysopeplus] aureoventris* (fig. 68) (latitude 27° S) and *chrysopeplus* (latitude 27° N).

The southern allospecies of 16 superspecies occur farther south than do their northern allospecies to the north. Several cases involve species

reaching the cool south temperate region, but having northern allospecies that do not reach the cool north temperate region. These examples are: *Harpyhaliaetus [coronatus] coronatus* (latitude 41° S) and *solitarius* (latitude 27° N), *Coccyzus [minor] melacoryphus* (latitude 37° S), and *minor* (latitude 28° N), *Glaucidium [brasili-anum] nanum* (fig. 30) (latitude 55° S) and *brasilianum* (latitude 34° N), and *Carduelis [magellanica] magellanica* and *barbata* (latitude 41° and 55° S respectively) (fig. 79), and *C. [magellanica] notata* (latitude 31° N). The failure of *Harpyhaliaetus solitarius* to range northward in the western Nearctic is particularly notable, as habitats seem favorable and it has no close, possibly competitive relatives in the north. It is also difficult to understand the weak northward distribution of *Jacana [spinosa] spinosa* (to latitude 25° N, compared with latitude 35° S for its allospecies *J. jacana*), and *Cyanocompsa [cyanea] parellina* (to latitude 22° N, versus latitude 31° S for *C. cyanea*, its southern allospecies, fig. 69).

The observed differences in northward and southward extent of allospecies, of subspecies, and even of monotypic forms (usually species, but sometimes the same subspecies of a polytypic species) probably are attributable largely to intrinsic (genetic) differences between the populations, and to historical factors involved in their access to suitable habitat, as noted above. Some forms not reaching Middle America or only partly distributed northward along that narrow neck of land undoubtedly have only recently reached Middle America from South America. The tenuous distribution of various tropical habitats in Middle America may impede further the northward movement of these forms. In some cases competitors may have limited northward distribution of species, especially in cases of geographical replacement by northern allospecies within superspecies (e.g., *Botaurus [stellaris]*, *Accipiter [bicolor]*). The most puzzling cases are those in which forms having no close relatives in the Nearctic attain a wide distribution in South America including the southern part of the continent, and reach (or their allospecies reach) North America but fail to penetrate far into it. Examples include *Polyborus plancus*, *Falco femoralis*, *Pitangus sulphuratus*, and *Harpyhaliaetus [coro-*

natus]. In some instances their extension into North America may have been very recent.

The frequent occurrence of chaco species in surrounding regions is readily explainable on the basis of ease of access. Their southward distribution tends to be restricted considerably by the sharp reduction of forest and woodland habitats in the pampas and central Andes of Argentina. Relatively few species have reached (or have managed to survive in) the Fuegian forest, which is isolated from more northern forest formations, the nearest of which is the chaco.¹ Species favoring riparian woods, edges, chaco scrub, and small bushes and trees frequently penetrate the pampas to northern Buenos Aires, or even Río Negro, but, as noted, few reach the Fuegian forest region.

Chaco Birds Reaching the Old World

Chaco species reaching the Old World include four species widely distributed in North America, and which probably achieved a New World or an Old World (depending upon their origin) connection via North America. These are *Gallinula chloropus*, *Gallinago gallinago*, *Tyto alba*, and *Asio flammeus*. Another three inhabitants of the chaco reaching the Old World also extend into North America, but have a southerly distribution there, suggesting that they reached that continent from the south (the herons *Nycticorax nycticorax* and *Egretta alba*, and *Dendrocygna bicolor*). Four other species occur in Africa and in three cases Asia as well, but they do not reach North America (*Butorides striatus*, *Dendrocygna viduata*, *Sarkidiornis melanotis*, and *Larus cirrocephalus*). Transatlantic relationships of intraspecific populations of at least four and perhaps as many as seven species (about one-seventh as many species as reach North America) suggest a regular, long-term transfer of species between Africa and the New World. Historical factors suggest that this transfer has been diminishing throughout the Tertiary, so that in the late Tertiary it has involved only larger species, water birds, and long-distance migrants. Earlier invaders

¹Indeed some Fuegian species such as *Picoides lignarius* and *Campephilus magellanicus* have their nearest relatives in the chaco (*P. mixtus* and *C. leucopogon*, respectively).

of South America from Africa probably include the ancestors of New World species of *Cairina*, *Vanellus*, and *Ceryle* and possibly the ancestors of *Platalea ajaja*, *Spiziapteryx circumcinctus*, and *Athene cunicularia*.

ENDEMICITY IN THE CHACO

Chaco birds exhibit very little endemism. Only one species, *Eudromia formosa*, is confined to the chaco, and, indeed, only five subspecies, all of the sedentary rheas and tinamous, are confined to the chaco. In addition to *Eudromia formosa*, species largely restricted to the chaco are *Ortalis canicollis*, *Dryocopus schulzi* (fig. 37), and *Pseudocolopteryx dinellianus*. Eight other species (*Chunga burmeisteri*, fig. 24, *Aratinga nenday*, *Campephilus leucopogon*, *Furnarius cristatus*, *Phacellodomus sibilatrix*, fig. 40, *Paroaria capitata*, fig. 67, *Lophospingus pusillus*, fig. 73, and *Saltatricula multicolor*, fig. 78) have half to three-quarters of their ranges in the chaco. The majority of these species extend beyond the chaco to the south (chaco scrub), the southwest (Tucumán), the southeast (eastern "chaco" extension), or the east (pantanal, riparian).

Subspecies endemic to the chaco are *Rhea americana araneipes* (fig. 11), *Nothura maculosa chacoensis*, *N. m. pallida* (fig. 16), *Eudromia formosa formosa* (fig. 17), and *E. f. mira*; *Nothura maculosa paludivaga* and *Colaptes melanochloros nigroviridis* are almost entirely restricted to the chaco. Eleven other species have races with ranges 60 to 80 percent within the chaco. These forms (*Nystalus maculatus striatipectus*, fig. 32, *Picumnus cirratus pilcomayensis*, fig. 33, *Picoides mixtus malleator*, fig. 34, *Celeus lugubris kerri*, *Campephilus l. leucopogon*, *Xiphocolaptes m. major*, *Campylorhamphus trochilirostris hellmayri*, fig. 38, *Upucerthia certhioides estebani*, *Thamnophilus caerulescens paraguayensis*, *T. c. dinellii*, fig. 42, and *Thraupis sayaca obscura*, fig. 61) largely extend beyond the chaco to the west (subtropical dry forest), the south (chaco scrub), and the east (riparian woodlands, chaco ecotone with southeastern Brazilian forests).

The markedly low endemism, involving but one of the 409 species and five (or seven) of approximately 337 subspecies (these represent

276 polytypic species of the chaco) occurring in the chaco, indicates that this region is and has been easily and directly accessible to surrounding biotic communities, and that its avifauna as a result is derived from elsewhere. Much of the chaco may have been inundated or otherwise modified greatly in the past, and its present fauna may be so recently derived that there has been no opportunity for differentiation. Finally, its very close affinities with surrounding avifaunas make the "chaco avifauna" a nonentity, the term being useful only in a strictly distributional context.

AVIAN DISTRIBUTION IN THE CHACO AND SURROUNDING REGIONS

I propose to examine the patterns of geographical ranges exhibited by chaco birds, the question asked being: in what direction(s) and into which regions do chaco birds extend? Turning our attention to the initial part of this question, we first exclude from consideration here the endemic chaco species (see above), a few species almost entirely restricted to the chaco, and, for the time being, the "fringe" species that barely reach the chaco and may or may not breed within it.

A great number of chaco birds occur more or less throughout the chaco, and these may be considered first. A total of 141 species have ranges including the entire chaco, and 43 others occupy more than 80 percent of it. Not surprisingly, a majority of these species (105 of the 184 total) are nonpasserine, generally larger and tending to occupy greater ranges than passerine species. Species are found in habitats suitable for them, of course, such that broadly ranging chaco species vary greatly in their abundance, and indeed in their occurrence in different parts of the chaco. Larger birds of prey and other species may be limited in availability of nest sites or other factors that cause them to be spottily distributed. As another example, birds requiring open water are numerous among wide-ranging chaco species; no less than 45 species are water-dependent to this degree. Included are the various grebes, ciconiiform birds, ducks, a few hawks (*Rostrhamus sociabilis*, *Busarellus nigricollis*), most rails, three shorebirds, a gull, kingfishers, and at least two

passerine birds (*Fluvicola pica*, *Agelaius ruficapillus*). Such birds are restricted, especially during the breeding season, to the vicinity of marshes, ponds, and rivers, and hence they may be expected to have a very local distribution. Too little is known of the chaco to indicate their precise distributions, but they must be more numerous in the wetter eastern chaco, and in esteros of the ecotonal (with pampas) southern chaco. As the spring wet season and the breeding season more or less coincide, these water-dependent birds can breed locally even in the "dry" central chaco. Parenthetically, much of the chaco must be deserted by these species during the drier periods of the year.

Of the 184 species essentially occupying the entire chaco, 31 are so widespread as to extend beyond it a great distance in every direction, including westward into at least the lower Andes. The 153 species extending beyond the chaco in less than all directions generally tend to extend northward, eastward, and southward. Species extending beyond the chaco only within the 180 degrees comprising the western two quadrants number 12, those passing only to the south, 28, to the east, 38, and to the north, 24. More specifically, the following number and percentage of the 153 species extend outward from the chaco in the directions stated: S, 98 (64%); SE, 102 (67%); E, 104 (68%); NE, 107 (70%); N, 78 (51%); NW, 77 (51%); W, 10 (7%); and, SW, 59 (38%). Thus, most species extend beyond the chaco between northwestward and southward, and few occur beyond it very far to the west or southwest. Otherwise, no clear picture emerges, for it appears that widespread species which are able to occupy the chaco also find surrounding regions suitable for their needs. Indeed the single most frequent pattern of distribution (26 species) among these is that of species extending from northwest to north, and around the eastern quadrants to the south, and southwest. Most other species show somewhat to very restricted patterns (e.g., north to east, northwest to southeast, etc.) within this basic pattern, and only 10 species have a western distribution falling outside of the basic pattern.

The wide-ranging species that occupy all or most of the chaco give us some idea of a general pattern of distribution, but species with more

restricted avian distributions provide more details. What parts of the chaco are occupied by the 194 species with restricted distributions therein, and what are the directions in which these species extend beyond the chaco? In seeking answers to these questions, I shall consider continuous distributions, leaving disjunct distribution patterns for later.

A frequent pattern (34 examples) of these restricted-range species is a distribution in the western, northern, and eastern chaco, with gaps in the central and southern chaco. This pattern presumably relates to requirements for more humid, less dry conditions. Most of these species are tropical in distribution, hence they extend northwestward to eastward beyond the chaco. In a few instances (e.g., *Chondrohierax uncinatus*, *Herpetotheres cachinnans*, *Ara ararauna*) they extend only northwestward to northeastward, that is, their southernmost limit is reached in the chaco. The rather strictly tropical orientation of the ranges of the bulk of the species showing this pattern is indicated by the fact that only three (*Syrigma sibilatrix*, *Piaya cayana*, and *Elaenia parvirostris*) of the 34 are distributed south of the chaco to the southeastward as far as Uruguay. Two exceptional species with this pattern of distribution in the chaco are the widespread *Cathartes aura* (see Olrog, 1959) which is the only species extending westward to a considerable degree, and *Accipiter bicolor*, with a northwestern to eastern extension beyond the chaco, but also having a disjunct in the southern Andean region of Chile and Argentina. These are the only two species of broad occurrence in temperate South America. Finally, I should note that *Melanopareia maximiliani*, whose chaco distribution fits into this pattern, extends far beyond the chaco only to the northwest (La Paz, Bolivia); probably half its range is in the chaco.

The most frequent pattern (38 species) observed among species only partly occupying the chaco is restriction to the eastern chaco. These species occupy 50 percent or more of the eastern edge of the chaco; most occur in the pantanal and the eastern fringe of moist chaco woodland bordering the pantanal. The purely pantanal species include the water birds of the Paraguay River and its tributaries (near their mouths), marsh-edge species, and grassland birds. Two species

(*Aratinga nenday* and *Attila phoenicurus*, fig. 44) extend westward through most of the eastern chaco woodlands. Four additional species, not included among the 38, occur throughout the eastern chaco and at least locally westward into the central chaco. Three of these are water-dependent species (*Alectrurus risora*, *Agelaius cyanopus*, *Amblyramphus holosericeus*) to be found about the few esteros and perhaps only seasonally in the central chaco, and the other is the brushland edge *Anumbius annumbi*. The species restricted to the eastern chaco extend in various directions from north and northwest to south. Several species (*Porphyryla flavirostris*, *Columba speciosa*, *Amazilia chionogaster*, and *Elaenia flavogaster*) reach their southern limit in the Paraguay River corridor and in the eastern chaco. Nine of the species extend south or southeast from the eastern chaco. Some of these are water birds (e.g., *Sterna superciliaris*), and others (e.g., *Sturnella superciliaris*) occur in the pampas. Only one (fig. 13), *Rhynchotus rufescens*, reaches south as far as northern Patagonia. Most of the 38 species extend eastward into Misiones, and southern Brazil, and to the northeast as well.

Twelve species occur only in the northern chaco (all or a combination of Santa Cruz, Bolivia, northern Paraguay, Mato Grosso, and in four cases as far south as Formosa or Salta, Argentina). These are of course northern (tropical) species, extending mainly northward, and to some degree northwest and northeast from the chaco. Included are such species as *Nothura boraquira* (fig. 15), *Aburria pipile*, *Pseudoseisura cristata* (fig. 41), *Herpsilochmus pileatus* (fig. 43), and a single higher oscine, *Nemosia pileata*. Nine species occur in the northeastern chaco (eastern and northeastern Paraguayan chaco, Mato Grosso, and, sometimes Santa Cruz), and these extend north and northeast (one east, also) from the chaco. Some examples are *Pyrrhura molinae*, *Glaucidium minutissimum*, *Campephilus melanoleucos*, *Basileuterus flaveolus* (fig. 59), and *Tersina viridis*.

In addition to the northern, northeastern, and eastern chaco species of restricted distribution in the chaco, 26 species occur in all or parts of both the northern and the eastern chaco. These also include species chiefly having tropical affinities, either northward or northward and eastward

(southeastern Brazil). *Ara chloroptera* actually reaches its southern limit in the eastern chaco, and *Fluvicola leucocephala* does so in the pantanal of the eastern chaco and adjacent Argentine Mesopotamia. The very few species of this group which extend southward beyond the limits of the chaco (actually southeastward to Buenos Aires and Uruguay) are the widespread *Stelgidopteryx ruficollis*, and the Neotropical *Gnorimopsar chopi*, *Cacicus chrysopterus*, *C. solitarius*, and *Sporophila leucoptera*. *Polyborus chimachima* is replaced south of the chaco by its allospecies *P. chimango*.

In contrast to the great number of species restricted to the northern and eastern chaco, only two species, *Colaptes campestris* (fig. 36) and *Pseudocolopteryx flaviventris*, occur through the eastern and southern chaco. These species extend beyond the chaco to the northeast, east and south (*C. campestris*), and to the south (*P. flaviventris*). Fifteen species occur only within the southeastern chaco (southern Paraguay or Formosa southward to Santa Fe, and west in some to Santiago del Estero), extending beyond it to the east (six species), to the northeast and east (*Elaenia mesoleuca*, fig. 51), to the northeast to southeast (*Eleothreptus anomalus*, *Xolmis dominicana*, and *Pseudoleistes guirahuro*), to the east and south (*Pseudoleistes virescens*), to the southeast (*Agelaius flavus*), or to the south (*Heteronetta atricapilla*, *Gubernatrix cristata*, and *Aimophila strigiceps*, fig. 41).

Species more or less restricted to the southern chaco during the breeding season number 26. Of these, 12 extend well into the central chaco, reaching Formosa or even southern Paraguay. One of them (fig. 20), *Spiziateryx circumcinctus*, seems confined to the xeric central chaco corridor, from which it extends directly south in the chaco scrub. The bulk of the 26 species are southern species which reach their northern limit in the chaco. One species with a very limited range (*Pseudocolopteryx dinellianus*) extends only westward from the chaco. Five species (*Knipolegus aterrimus*, *Progne modesta*, fig. 54, *Cistothorus platensis*, *Thraupis bonariensis*, and *Poospiza torquata*) occur south of the chaco, but also extend northward varying distances along the Andes (or west of them) to the west of the chaco. The remaining 20 "southern" species

extend directly south from the chaco (three chaco scrub species, e.g., *Coryphistera alaudina*), mainly to the south and southeast (seven open, wet country birds, including *Molothrus rufaxillaris*), mainly to the southwest (*Furnarius cristatus*), or southwest to southeast in suitable habitats (nine species, e.g., *Polyborus chimango*, *Drymornis bridgesii*, and *Hymenops perspicillata*).

Seven species enter the chaco from the southwest, and three of these reach the central chaco (Paraguay). The Andean *Nothura darwinii* (fig. 16), and the southern *Eudromia elegans* (fig. 17), *Knipolegus striaticeps*, and (fig. 49) *Stigmatura budytoides* (the last has a disjunct eastern Brazilian population, discussed below) reach only the southwestern edge of the chaco. The allospecies of *E. elegans*, *E. formosa*, extends northeastward (fig. 17) in the chaco from the range of *elegans* (*E. formosa* is endemic in the chaco). Reaching farther northeastward into the chaco from the southwest are *Chunga burmeisteri* (fig. 24), *Dryocopus schulzi* (fig. 37), and *Serpophaga nigricans*.

Strix rufipes (fig. 31) and *Serpophaga subcristata* (fig. 50) occupy the southern and most of the western chaco (north to Salta or western Paraguay). The former species extends southwestward from the chaco, and the latter ranges widely from the northeast to the south and southwest of the chaco.

Two chaco birds (*Buteo leucorrhous*, *Phacellodomus striaticollis*) show an apparent disjunction in the southern chaco, occurring in the southwest and the southeast, with a gap in the south-central portion. Likewise, five species show east-west chaco disjunction, being restricted to the eastern and western portions of the chaco. *Penelope obscura* and *Arremon flavirostris* (fig. 75) extend predominantly east and northeast from the chaco, but are also found disjunctly from Bolivia to Catamarca, Argentina, west of the chaco. *Ramphastos toco* and *Dryocopus lineatus* are widespread north of the chaco; the former extends southward to the west of the chaco and in its western fringes, as well as to Santa Fe in the east, and *D. lineatus* is found along the eastern border of the chaco in Mato Grosso and Chaco Province, and as an isolate (from central Bolivia) in Tarija, Bolivia. *Poospiza nigrorufa* is a

southern species, occurring disjunctly from Salta and western Santiago del Estero (also La Paz and Cochabamba, Bolivia) southward in the west (to western Córdoba and La Rioja), and from southern Paraguay and Chaco Province (also Rio Grande do Sul, Misiones) south to Río Negro in the east.

No species are restricted within the chaco to its western edge. However, 12 species do occur in the western chaco and in the northern chaco, but do not extend southward in the eastern chaco. Some of these reach southward only to Salta in the west, and others extend into Santiago del Estero (*Phacellodomus rufifrons*, *Batara cinerea*, and *Contopus cinereus* only questionably to Santiago del Estero), or farther (*Dendrocygna autumnalis*). Other examples of these species are: *Neochen jubata*, *Ara auricollis*, *Trogon curucui*, *Synallaxis scutatus*, and *Inezia inornata*. Most of the 12 species are widely distributed to the north, and even (e.g., *Contopus cinereus*) northeast of the chaco, but *Inezia inornata* occurs only from Salta north to Bolivia and east to Mato Grosso.

The pattern shown by the chaco species with restricted ranges in the chaco is similar to that analyzed above for the species inhabiting all the chaco. Of the 194 species, 140 occur in parts of the eastern chaco (72%), 93 in the northern chaco (48%), 63 in the western chaco (32%; 46 of the 63 also occur in the northern chaco, and 34 of these in the eastern chaco, as well), and 55 in the southern chaco (28%). There is a greater emphasis on northern and eastern, and less emphasis on southern distributions compared with the widespread chaco species, but otherwise the overall pattern is similar. The lessened southern influence and greater northern and eastern influence shown by species with restricted chaco distribution seem to indicate that widespread species tend not to reach the limit of their range at the edges of the chaco, that northern or northeastern species often reach their southwestern limit in the chaco, and that southern species reaching the chaco, particularly from the pampas, extend north in the eastern chaco as well as in the southern chaco, and hence they are not exclusively restricted within the chaco to its southern quadrants.

The 22 "fringe" species barely (and question-

TABLE 1
Occurrence of Chaco Species in Other Regions^a

Region	Nonpasserines	Passerines	Total
Regions Adjacent to the Chaco			
Campo-Cerrado	175	136	311
Argentine Mesopotamia	148	155	303
Western Amazonia	159	141	300
Dry Subtropical Forest	151	138	289
Pampas	122	118	240
Chaco scrub	90	92	182
Regions Distant from the Chaco			
Caatinga	141	107	248
Southeastern Brazil	139	98	237
Guianan highlands	123	75	198
Lower Amazon	118	80	198
Llanos	114	68	182
Lower Orinoco	118	64	182
Northeastern Colombia- Northwestern Venezuela	113	65	178
Eastern Brazil	105	59	164
Central sub-Andean forests	82	73	155
Northwestern Peru- Southwestern Ecuador	61	34	95
Patagonia	52	23	75
Central Chile	42	6	48
Andean highlands	30	11	41

^aSee text for definition of the regions listed here.

ably) reaching the chaco do so mainly from the north (seven species), northeast (12 species), and east (six species). Eighteen of the 22 species are apt to reach the chaco in the northeast quadrant, and 16 of them exclusively there. The only species reaching the fringe of the southern chaco in either southern quadrant is the Andean swift, *Cypseloides rothschildi*, which may reach the southwestern chaco—it is not a southern bird. All the other species are tropical, reaching the fringe of the chaco from the north, generally. *Hemithraupis guira* and *Sporophila hypochroma* may enter the chaco disjunctly in the west and east, and in the northwest and east, respectively.

In addition to noting the directions in which the ranges of chaco birds extended beyond the chaco, I established the occurrence of chaco species in 19 more or less ecologically defined regions (table 1) of South America. These regions are described in the following discussion.

Immediately adjacent to, hence directly accessible to, the chaco are six distinct regions. To the north of the chaco, and not separated from it by any barrier is western Amazonia, the region including all of the upper Amazon drainage in Brazil, southeastern Colombia, eastern Ecuador, eastern Peru, and northeastern Bolivia. Northeast of the chaco in Mato Grosso is the vast region of the campos and its associated forests (cerrado and cerradão), extending to Maranhão, Goiás, western Bahía, and western Paraná. I have not included eastern Paraguay in table 1, because it is ecotonal between campo (north, northeast), pantanal and chaco (west), southeastern Brazilian forest (east, southeast), and pampas (south-central). To the southeast, the wet region of Argentine Mesopotamia (Corrientes, Entre Ríos) is included in the analysis. Spread over a larger area than eastern Paraguay, it is ecotonal (chaco in the west and even across

the south-central portion, wet pampas in the central portion, and southeastern Brazilian forest along the major rivers and in the northeast), but also is distinct by virtue of its vast wet areas. These include much of central Corrientes (Esteros del Iberá and surrounding wet area), and all of southern Entre Ríos (the Río de la Plata delta region between the Uruguay and Parana rivers). Southeast of the chaco from Santa Fe to Buenos Aires and Uruguay is the pampas region. Directly south of the south-central chaco is the chaco scrub region, which extends in an arc through Córdoba and then southeast through La Pampa and western Buenos Aires to northeastern Río Negro. Finally, west of the chaco along its entire western border is the dry subtropical forest of the lower Andean slopes from central Bolivia to Catamarca, Argentina. Perusal of table 1 should make it clear that the strong tendency of chaco birds to extend beyond the chaco northward to eastward is due to the influence of three major adjacent regions in those directions. More chaco species extend into these regions, the campo-cerrado, Argentine Mesopotamia, and western Amazonia, than into any other adjacent or more distant region. Three-quarters of chaco species extend into the campo-cerrado region, nearly three-quarters extend into Argentine Mesopotamia and western Amazonia, between half and three-quarters of the species extend into the dry subtropical forest, and somewhat less than half extend into the chaco scrub region.

Among the regions more removed from the chaco, the xeric caatinga region of Bahía, Ceará, and Piauí is occupied by 248 chaco species, more than the number found in all other regions, including the southeastern Brazilian forest (Rio de Janeiro to Rio Grande do Sul coastally, and inland as far as western Paraná, and Misiones, Argentina), which is much nearer the chaco. The caatinga also numbers among its avian inhabitants more chaco species than found in the pampas or chaco scrub, both adjacent to the chaco. Thus, the orientation of the ranges of chaco species toward the northeast may be partly attributable to the relationship of the chaco and caatinga avifaunas, as well as to affinities with the campo-cerrado avifauna.

The southeastern Brazil region (including both lowland-slope forest and upland araucaria pine

forest) is the home of nearly as many chaco species as the pampas, or caatinga. Most of the eastern chaco (Paraguay River) species reach the southeastern Brazilian forests. Among the other regions to be considered, those having within their limits from 38 to 48 percent of chaco species are as follows: The Guianan highlands (southeastern Venezuela, adjacent Guiana and Surinam, 198 species); the Lower Amazon region (area adjacent to the river and east of Obidos, 198 species); the llanos of southwestern Venezuela and adjacent Colombia (182 species); the lower Orinoco River region of Venezuela (182 species); the arid Guajira Peninsula, adjacent Zulia, and Falcón of Venezuela, forming the northeastern Colombia-northwestern Venezuelan region (178 species); coastal eastern Brazil (Rio Grande do Norte, 164 species); and, the central sub-Andean forests (Peruvian subtropical and montane forests, 155 species). All of these areas, relatively distant from the chaco, bear as many, or nearly as many chaco species as the chaco scrub region. The rather high number of species for the Guianan highlands, compared with the central sub-Andean forest slopes is interesting, suggesting that subtropical chaco species may have distributed themselves to (or from) the Guianan highlands by "ringing" the Amazon basin from the east (lower Amazon Valley, caatinga), rather than along the Andes.

Rather few chaco species (less than 25%) occur in the arid zone of the northwestern Peru-southwestern Ecuador (95 species), in Patagonia south of the Río Negro (75 species), in central coastal Chile (48 species), and in the Andean highlands (puna zone, 41 species). The occurrence of chaco species in northwestern Peru in numbers greater than in Patagonia suggests that chaco birds have been able to reach xeric scrub habitats all over the continent, although the far greater number of chaco species (178) reaching arid northeastern Colombia and northwestern Venezuela stresses the effectiveness of the Andes in curtailing east-west movement.

Nonpasserine species comprise over half (53%) of the chaco avifauna. This percentage roughly is maintained in the regions adjacent to the chaco, with variation from 50 percent (chaco scrub) to 56 percent (campo-cerrado), except for Argentine Mesopotamia, where a majority (54%)

of chaco species are passerines. As expected because of their greater distance from the chaco, the proportion of nonpasserine chaco species in more distant regions of South America is greater. Regions relatively close to the chaco show 53 percent (central sub-Andean forests) to 60 percent nonpasserine, chaco species. More distant areas show from 62 percent (Guianan highlands) to 68 percent (llanos) nonpasserine, chaco species. Exceptions to these limits of variation are the cool and rather open Patagonian region, somewhat close to the chaco but with 69 percent nonpasserines, the treeless Andean highlands, also close to the chaco, and having 73 percent nonpasserines, and, demonstrating the efficacy of the Andes Mountains as a barrier to small birds, 88 percent nonpasserine chaco species in central (coastal) Chile.

I conclude that birds found in the chaco tend to be widespread in South America, especially in arid scrub, ecotonal (forest-savanna), and forested regions. They extend north, northeast, and east beyond the chaco to a greater extent than to the west and south. Passerine species tend to range less widely than do nonpasserine species, they occur to a much lesser extent in treeless, cool regions, and they are affected to a greater degree by mountain barriers than are nonpasserine, chaco species.

MAJOR DISJUNCTIONS IN RANGE AMONG BIRD SPECIES OCCURRING IN THE CHACO

The continuous ranges of chaco birds having been treated above, it remains to consider discontinuities, or disjunctions in the ranges of these birds. Both intraspecific and interspecific (i.e., between allospecies of a single superspecies) range disjunctions of large scale, that is, involving over 100 miles of separation, will be analyzed in this section. Disjunction in range implies the existence of unsuitable habitat presently intervening between populations that formerly were connected. Unless there are indications that the geographically isolated populations have undergone marked shifts in habitat preferences, one must assume that the various habitats presently occupied by the isolated populations roughly encompass the range of preferred habitats in the

recent past, i.e., since the barrier was interposed, as well as at present. Species with restricted distributions, particularly those species occurring in a limited spectrum of habitats, generally are of greater importance to the zoogeographer than are species with broader distributions and species occurring in diverse habitats. Of special significance are nonmobile species restricted in habitat preference, and occurring in disjunct populations in structurally (physiognomically) similar habitats.

Prior to the discussion of these species it is pertinent to list the various species showing such disjunctions, categorized geographically. These lists follow in the order of conspecific disjuncts, then allospecific disjuncts. Asterisks in the first list indicate that the disjunct populations have differentiated into recognizable subspecies.

CONSPECIFIC RANGE DISJUNCTION

Western South America

Colombia to central Peru or northern Chile.—*Parabuteo unicinctus**, *Gallinula chloropus** (fig. 22), *Myiophobus fasciatus**.

Northwestern South America (western Peru or western Ecuador to Venezuela or Guianas).—*Podilymbus podiceps*, *Botaurus pinnatus*, *Dendrocygna autumnalis*, *Buteo leucorrhous*, *Molothrus bonariensis**.

Western Colombia or Middle America to western Ecuador or western Peru.—*Neocrex erythrops**, *Laterallus melanophaius**, *Vireo olivaceus**, *Euphonia musica**, *Piranga flava**.

Central western Peru to (in three cases) northern Chile.—*Neocrex erythrops**, *Columbina minuta*, *Glaucidium brasilianum* (fig. 30), *Philydor rufosuperciliatus**, *Progne modesta** (fig. 54), *Anthus lutescens**.

Highland southern Colombia to northern Peru and, contiguously, lowland southwestern Peru to southern Peru.—*Carduelis magellanica** (fig. 79).

Western Colombia-Middle America.—*Micrastur ruficollis**, *Columbina minuta**, *Glaucidium minutissimum**, *Lurocalis semitorquatus**.

Western Ecuador to northern Chile.—*Pyrocephalus rubinus**.

Southwestern Ecuador to southern Peru.—*Contopus cinereus** (fig. 47).

Southwestern Colombia to northwestern Peru.—*Cyclarhis gujanensis**, *Parula americana**.

Coastal western Ecuador to northwestern

Peru.—*Dendrocygna bicolor*, *Rynchops nigra*.

Western-eastern Ecuador.—*Notharcus macrorhynchus**, *Pyriglena leuconota**.

Southwestern Ecuador and Marañón Valley of Peru.—*Euscarthmus meloryphus**, *Geothlypis aequinoctialis**.

Coastal and riverine southwestern Ecuador or northwestern Peru, or both.—*Cairina moschata*, *Sarkidiornis melanotos*, *Rallus maculatus*, *Larus cirrocephalus*, and *Phaetusa simplex*.

Arid scrub of southwestern Ecuador, or northwestern Peru, or both.—*Gamponyx swainsonii*, *Spizaetus ornatus**, *Columbina talpacoti**, *Caprimulgus parvulus**, *Phaeomyias murina**, *Hemithraupis guira**, *Sicalis flaveola** (fig. 72).

Northern South America

Widespread, Amazon River to Eastern Colombia or northern Colombia and Guianas.—*Hylocharis sapphirina*, *Cacicus haemorrhous*, *Emberizoides herbicola**.

Eastern Peru, eastern Colombia, Venezuela, Guianas.—*Asio clamator**, *Phacellodomus rufifrons** (fig. 40), *Hirundinea ferruginea**, *Tachyphonus rufus* (fig. 62).

Non-Amazonian northern South America, northern Colombia to Guianas.—*Jabiru mycteria*, *Buteo albicaudatus**, *Rallus maculatus*, *Gallinula chloropus* (fig. 22), *Vanellus chilensis** (fig. 21), *Gallinago undulata*, *Podager nacunda**, *Fluvicola pica** (fig. 46), *Pyrocephalus rubinus**, *Tyrannus savanna**, *Myiophobus fasciatus**, *Euscarthmus meloryphus**, *Polystictus pectoralis** (fig. 48), *Sublegatus modestus**, *Parula americana**, *Sicalis flaveola* (fig. 72), *Ammodramus humeralis** (fig. 76).

Northeastern Andean slopes to Guianas.—*Dendrocygna bicolor*, *Caprimulgus cayennensis**, *Contopus cinereus** (fig. 47).

Southern or southeastern Venezuela, or Guianan highlands or both.—*Attila phoenicurus* (fig. 44), *Pachyramphus viridis**, *Contopus cinereus** (fig. 47), *Todirostrum margaritaceiventer**, *Stelgidopteryx fucata*, *Geothlypis aequinoctialis**, *Chlorophonea cyanea**, *Euphonia musica*, *Junco capensis**, *Carduelis magellanica** (fig. 79).

Northern Venezuela, Lower Orinoco, Guianas.—*Poliolimnas flaviventer*, *Chaetura andrei**, *Xenopsaris albinucha* (fig. 45).

Lower Orinoco region or Guianas, or both.—*Circus buffoni*, *Parabuteo unicinctus**, *Spizastur melanoleucos*, *Falco deiroleucus*, *Laterallus melanophaius*, *Columbina squammata*, *Columbina minuta*, *Glaucidium minutissimum*, *Lurocalis semitorquatus**, *Colaptes campestris* (fig.

36), *Empidonax euleri**, *Anthus lutescens**, *Piranga flava*, *Thlypopsis sordida** (fig. 63), *Cissopis leveriana* (fig. 64).

Guianas and northeastern Amazonian Brazil.—*Polytmus guainumbi**.

Llanos, northern or northeastern Colombia to northern Venezuela or Guianas.—*Theristicus caudatus*, *Phimosus infuscatus**, *Columbina squammata**, *Athene cucularia**, *Machetornis rixosus**, *Icterus icterus**.

Llanos to northern Venezuela or Guianas.—*Syrigma sibilatrix**, *Buteo brachyurus*, *Porzana albicollis*, *Neocrex erythrops*, *Porphyriops melanops**, *Xenopsaris albinucha* (fig. 45), *Anthus lutescens**, *Geothlypis aequinoctialis**, *Basileuterus flaveolus* (fig. 59), *B. culicivorus** (fig. 60), *Hemithraupis guira**.

Llanos, Orinoco Valley, Guianas.—*Sarkidiornis melanotos*, *Elanus leucurus*.

Llanos and arid northeastern Colombia—northwestern Venezuela.—*Plegadis chihi* (fig. 18).

Southeastern Colombia.—*Helimaster fuscifer*.

North-central Colombia (Lower Magdalena Valley, adjacent mountains).—*Porzana albicollis*, *Poliolimnas flaviventer**, *Gallinago undulata*, *Forpus xanthopterygius**, *Cnemotriccus fuscatus**, *Todirostrum margaritaceiventer**, *Cistothorus platensis**, *Geothlypis aequinoctialis**, *Sporophila lineola**.

Cauca Valley, or Upper Magdalena Valley, or both (Colombia).—*Elanus leucurus*, *Poliolimnas flaviventer*, *Columbina talpacoti*, *Athene cucularia**, *Notharcus macrorhynchus**, *Pyriglena leuconota**, *Todirostrum margaritaceiventer**, *Basileuterus flaveolus* (fig. 59), *B. culicivorus** (fig. 60), *Hemithraupis guira**, *Cyanocompsa cyanea** (fig. 69), *Ammodramus humeralis** (fig. 76), *Carduelis magellanica** (fig. 79).

Northern Colombia to northern Venezuela.—*Sarkidiornis melanotos*, *Buteo brachyurus*, *Nemosia pileata**.

Arid northeastern Colombia or northwestern Venezuela, or both (to central-northern Venezuela in some).—*Micrastur ruficollis**, *Columbina talpacoti*, *Aratinga acuticauda** (fig. 27), *Dromococcyx pavoninus**, *Caprimulgus parvulus*, *Cnemotriccus fuscatus**, *Basileuterus culicivorus** (fig. 60), *Thraupis sayaca** (fig. 61), *Piranga flava** (last in mountains only).

Venezuela (except northwest) and Guyana.—*Piranga flava**.

Northern Venezuelan lowlands.—*Parabuteo unicinctus*, *Spizastur melanoleucus*, *Falco deiroleucus*, *Laterallus melanophaius**, *Dromococcyx pavoninus**, *Caprimulgus parvulus*, *Todirostrum margaritaceiventer**.

Mountains of northern Venezuela.—*Stelgidopteryx fucata*, *Cistothorus platensis** (to NE Colombian mountains), *Cyanocompsa cyanea** (fig. 69).

Amazonian Region

Widespread in western Amazonia (llanos to Bolivia and middle Amazon).—*Cissopis leveriana* (fig. 64).

Amazonian fringe, Guianas west to Ecuador and Amazonian western Brazil.—*Dromococcyx pavoninus*.

Lowland eastern Peru.—*Sarkidiornis melanotos*, *Falco deiroleucus*, *Lurocalis semitorquatus**, *Todirostrum margaritaceiventer**.

Western Amazonia (southeastern Colombia, eastern Peru, western Amazonian Brazil).—*Poliolimnas flaviventer*, *Laterallus melanophaius**, *Forpus xanthopterygius**, *Glaucidium minutissimum*.

Central Amazon Valley region, Brazil.—*Lurocalis semitorquatus* (to Lower Amazon), *Attila phoenicurus* (fig. 44), *Cyanocorax chrysops** (fig. 56), *Tersina viridis**, *Ammodramus humeralis** (fig. 76).

Lower Amazon Valley, mouth of Amazon River, Marajo Island.—*Porzana albicollis*, *Bubo virginianus*, *Glaucidium minutissimum*, *Picumnus cirratus** (fig. 33; to Guianas), *Colaptes melanochloros*, *Colaptes campestris* (fig. 36), *Pachyramphus viridis*, *Empidonomus aurantioatristatus** (to Pará, Maranhão), *Agelaius cyanopus** (isolates in Amapá, Maranhão), *Euphonia musica*, *Tachyphonus rufus* (fig. 62), *Sporophila caerulescens*, *Sicalis luteola**, *Coryphospingus cucullatus* (fig. 74), *Ammodramus humeralis** (two distinct races, fig. 76, isolated in upper part of lower Amazon River, and at mouth of that river), *Coryphaspiza melanotis** (fig. 73).

Amazon Valley (all).—*Harpagus diodon*, *Molothrus bonariensis**.

Sub-Andean (lower slopes) eastern Colombia to Bolivia, or parts thereof.—*Columbina minuta*, *Hydropsalis brasiliana*, *Herpsilochmus pileatus** (fig. 43, two isolates, eastern and southeastern Peru), *Formicivora rufa** (two isolates, north-central and eastern Peru, same race), *Pachyramphus viridis** (two isolates, eastern Ecuador, north-central Peru), *Turdus leucomelas*, *Chlorophonea cyanea**, *Piranga flava**, *Pheucticus aureoventris** (fig. 68, three isolates, separate races, in eastern Colombia, eastern Ecuador and adjacent Peru, and southeastern Peru, see below), *Carduelis magellanica* (fig. 79).

Southeastern Peru (sub-Andean or lowland).—

Knipolegus cabanisi (adjacent Bolivia), *Pyrocephalus rubinus**, *Stelgidopteryx fucata*, *Turdus leucomelas*, *Geothlypis aequinoctialis*, *Tachyphonus rufus* (fig. 62), *Pheucticus aureoventris** (fig. 68).

Northern Bolivia.—*Forpus xanthopterygius**, *Colibri serrirostris* (also eastern Bolivia), *Tachycineta leucorrhoa*, *Coryphaspiza melanotis* (fig. 73).

Eastern and Southern Brazil

Widespread in northeastern Brazil (caatinga, eastern campo, all northeastern region).—*Poliolimnas flaviventer*, *Porphyriops melanops*, *Nemosia pileata**.

Caatinga region (Ceará, eastern Bahia, Piauí).—*Nothura boraquira* (fig. 15), *Aramides ypecaha* (fig. 21), *Porzana albicollis*, *Columba picazuro** (fig. 25), *Aratinga acuticauda** (fig. 27), *Coccyzus cinereus* (fig. 29), *Glaucidium minutissimum*, *Schoeniophylax phryganophila**, *Pseudoseisura cristata* (fig. 41), *Myrmorchilus strigilatus* (fig. 15), *Xenopsaris albinucha* (fig. 45, to coastal Ceará), *Xolmis irupero**, *Stigmatura budyoides** (fig. 49), *Molothrus badius** (adjacent northeastern Brazil), *Icterus icterus** (adjacent campo and adjacent northeastern Brazil).

Northeastern corner of Brazil.—*Nothura maculosa** (fig. 16, Ceará), *Pyriglena leuconota**, *Elaenia spectabilis** (Fernando de Noronha Island), *Cyanocorax chrysops** (fig. 56, Pernambuco), *Vireo olivaceus** (Fernando de Noronha Island).

Rio de Janeiro.—*Rallus sanguinolentus**, *Piculus chrysochloros**, *Agelaius cyanopus**.

Southeastern Brazil.—*Picumnus cirratus** (also southeastern campo, southern caatinga, fig. 33).

Andean and Southern South America

Northern Andes, or central Andes, or both.—*Anas versicolor**, *Accipiter striatus**, *Buteo brachyurus**, *Spizastur melanoleucos*, *Falco deiroleucus*, *Gallinula chloropus** (fig. 22), *Lurocalis semitorquatus** (Colombian-Venezuelan Andes), *Chlorophonia cyanea** (southwestern Colombia), *Euphonia musica** (eastern Colombia), *Thraupis bonariensis**, *Saltator aurantiirostris** (fig. 66), *Sicalis luteola**, *Carduelis magellanica** (three races, in Colombia, in Venezuela and northeastern Colombia, and from southern Peru to northern Chile, plus another race in Ecuador and Peru as noted above under Western South America, see fig. 79).

Sub-Andean Bolivia.—*Melanopareia maximil-*

*iani** (northwestern Bolivia), *Stigmatura budyoides** (fig. 49), *Carduelis magellanica* (fig. 79).

Andes and southern South America.—*Theristicus caudatus**.

Chile or Chile and southern Patagonia.—*Accipiter bicolor**, *Parabuteo unicinctus*, *Gallinago gallinago**, *Strix rufipes** (fig. 31), *Pseudocolopteryx flaviventris* (central Chile), *Mimus triurus* (central Chile, may be casual only).

Patagonia.—*Netta peposaca* (Tierra del Fuego).

Chaco Region and Adjacent (Contiguous) Regions

South-central Bolivia (Tarija).—*Dryocopus lineatus* (fig. 37).

Eastern Bolivia (Santa Cruz).—*Hylocharis saphirina*, *Sporophila hypochroma*, *Carduelis magellanica**.

Mato Grosso.—*Amazilia chionogaster*, *Agelaius cyanopus* (two isolates, central-eastern and southeastern Mato Grosso).

Campo region.—*Aramides ypecaha* (fig. 21), *Coccyzus cinereus* (fig. 29), *Anumbius anumbi**.

Southeastern Brazil and adjacent Mesopotamian Argentina and eastern Paraguay.—*Notharcus macrorhynchus**, *Batara cinerea**, *Thamnophilus ruficapillus**.

Pantanal.—*Porzana flaviventer*.

Santa Fe.—*Colibri serrirostris*.

Chaco.—*Eudromia formosa** (species endemic to chaco, see fig. 17, two races isolated in north-central and southwestern chaco), *Fulica rufifrons*, *Amazilia chionogaster* (eastern Formosa), *Euscarthmus meloryphus* (eastern Formosa).

Subtropical dry forest (western Argentina, adjacent Bolivia).—*Rhynchotus rufescens** (fig. 13), *Penelope obscura**, *Porzana albicollis*, *Phacellodomus striaticollis**, *Arremon flavirostris** (also central Bolivia, fig. 75), *Aimophila strigiceps** (fig. 41, monte only), *Poospiza nigrorufa**.

Salta.—*Harpagus diodon*.

Tucumán.—*Buteo leucorrhous* (also Salta), *Poliolimnas flaviventer*, *Colibri serrirostris*, *Thalurania furcata*, *Elaenia flavogaster*, *Basileuterus culicivorus* (fig. 60).

DISJUNCTIONS AMONG ALLOSPECIES OF SUPERSPECIES

Western South America

Central western Peru.—*Otus [choliba] robotatus* (from *choliba* in west-central Colombia and eastern Peru).

Southwestern Ecuador to northern Chile.—*Sterna [albifrons] lorata* (from *superciliaris* in Amazonia, northern Venezuela), *Columbina [picui] cruziana* (from *picui* in northern Bolivia southward, and in central Chile).

Southwestern Ecuador to central-western Peru.—*Phytotoma [rutila] raimondii* (from *rutila* in north-central Bolivia, see fig. 53).

Southwestern Colombia to northwestern Peru.—*Campephilus [melanoleucos] gayaquilensis* (from *melanoleucos* in western Colombia, eastern Peru).

Coastal and riverine northwestern Peru.—*Tachycineta [albiventer] albilinea* (also disjunct in Middle America; from *albiventer* in northern Colombia and lowlands east of Andes).

Arid southwestern Ecuador, or northwestern Peru, or both.—*Fluvicola [nengeta] nengeta* (also disjunct in eastern Brazil; from *pica* in northern Colombia to the Guianas, and central Bolivia south and east, fig. 46), *Empidonax [albigularis] griseipectus* (from *euleri* in northeastern Colombia and lowlands east of the Andes), *Basileuterus [culicivorus] trifasciatus* (from south-central Colombia north and east through the lowlands east of the Andes, fig. 60), *Saltator [aurantiiostris] nigriceps* (from *aurantiiostris* in north-central Peru, fig. 66), *Poospiza [torquata] hispaniolensis* (from *torquata* in west-central Bolivia).

Northern South America

Widespread in northern South America to Guianas and Amazon Valley.—*Himantopus [himantopus] mexicanus* (south to Peru and Amazon Valley, from *melanurus* in southern chaco), *Amazona [aestiva] ochrocephala* (from *aestiva* in Bolivia, Mato Grosso and the caatinga), *Colaptes [punctigula] punctigula* (from *melanochloros* in Mato Grosso), *Serpophaga [nigricans] hypoleuca* (middle Orinoco and all Amazon Valley, from *nigricans* in Bolivia and the chaco), *Sturnella [militaris] militaris* (from *superciliaris* in Bolivia and campos), *Paroaria [gularis] gularis* (south to northern Bolivia, from *capitata* in chaco, fig. 67).

Northern Colombia to the Guianas.—*Crax [rubra] alector* (to lower Amazon, from *fasciolata* south of mouth of Amazon to caatinga and Bolivia), *Phaethornis [pretrei] augusti* (from *pretrei* in Maranhão and eastern Bolivia).

Southeastern Venezuela.—*Emberizoides [herbicola] duidae* (from *herbicola* at base of Mt. Duida).

Northern Venezuela to Middle and Lower

Amazon.—*Forpus [passerinus] passerinus* (from *xanthopterygius* in northern Colombia, western Amazonia and eastern Brazil).

Northern Colombia and northern Venezuela.—*Coccyzus [cinereus] pumilus* (from *cinereus* in Bolivia to caatinga and south, fig. 29), *Inezia [inornata] tenuirostris* (from *inornata* in northern Bolivia and Mato Grosso), *Coryphospingus [cucullatus] pileatus* (disjuncts in south-central and northern Colombia to northern Venezuela and caatinga region, which see, from *cucullatus* disjunctly in the Guianas and at the mouth of the Amazon, and in Bolivia and southern Brazil, fig. 74).

Arid northeastern Colombia, northwestern Venezuela, or both.—*Crypturellus [undulatus] cinnamomeus* (from *undulatus* in llanos and south, fig. 12), *Chauna [chavaria] chavaria* (from *torquata* in Mato Grosso and Bolivia, fig. 19), *Columba [corensis] corensis* (northeastern Colombia across northern Venezuela, from *picazuro* in caatinga, campos, and chaco, fig. 25).

Amazonian Region

Widespread in western Amazonia, llanos to northern Bolivia and middle Amazon.—*Crax [rubra] globulosa* (from *fasciolata* in lower Amazon, caatinga and central Bolivia).

Lower Amazon Valley and adjacent northeastern Brazil.—*Casiornis [rufa] fusca* (from *rufa* in campos, chaco).

Sub-Andean eastern Peru to Bolivia.—*Ara [maracana] couloni* (sub-Andean east-central Peru, from *auricollis* in northern Bolivia, fig. 26), *Synallaxis [azarae] azarae* (from *frontalis* in north-central Bolivia), *Basileuterus [flaveolus] signatus* (sub-Andean central Peru to Jujuy, Argentina, from *flaveolus* in south-central Colombia and the llanos, and in eastern Bolivia and northern Paraguay, fig. 59).

Southeastern sub-Andean Peru.—*Thamnophilus [ruficapillus] marcapatae* (from *ruficapillus* in central Bolivia).

Eastern and Southern Brazil

Widespread in northeastern Brazil, including caatinga region.—*Crax [rubra] blumenbachii* (eastern caatinga and adjacent coastal Brazil, from *fasciolata* in western caatinga and lower Amazon region), *Ara [maracana] maracana* (eastern campos eastward, from *auricollis* in chaco, fig. 26), *Fluvicola [nengeta] nengeta* (disjunct in eastern caatinga and adjacent areas, and in south-

western Peru region, which see; from *pica* in southern Mato Grosso, fig. 46), *Coryphospingus [cucullatus] pileatus* (disjuncts in caatinga, eastern campos and northern southeastern Brazil, and in northern Colombia and northern Venezuela, which see; from *cucullatus* in southern Brazil, chaco and Amazon mouth, fig. 74).

Caatinga.—*Polystictus [pectoralis] superciliosus* (southern caatinga, from *pectoralis* in Mato Grosso, fig. 48), *Paroaria [dominicana] dominicana* (caatinga and immediately adjacent northeastern Brazil, from *coronata* in chaco), *Embernagra [platensis] longicauda* (caatinga of Bahía, from *platensis* in Minas Gerais and Rio de Janeiro, fig. 77).

Southeastern Brazil.—*Cypseloides [niger] fumigatus* (from *rothschildi* in western chaco fringe), *Piculus [chrysochloros] aurulentus* (also adjacent eastern Paraguay and Misiones, from *chrysochloros* in Rio de Janeiro, and in caatinga, campos, and chaco).

Eastern and northeastern South America, southeastern Venezuela to southeastern Brazil.—*Pteroglossus [aracari] aracari* (from *castanotis* in southeastern Colombia, western Amazonia, eastern Mato Grosso and eastern Paraguay).

Andean and Southern South America

Northern Andes, central Andes or both.—*Nothura [perdicaria] pentlandii* (Ecuador to Argentina, from *cinerascens* in subtropical dry forest on lower eastern slopes of Andes, fig. 14), *Harpyhaliaetus [coronatus] solitarius* (northern Andes to southeastern Peru, from *coronatus* in eastern Bolivia), *Vanellus [chilensis] resplendens* (southern Colombia to Argentina, from *chilensis* in western and northern Colombia, and along eastern Andean slopes, fig. 21), *Gallinago [gallinago] andina* (central Peru to Argentina, from *gallinago* in lowlands east of the Andes, western Chile, and southern Andes), *Cypseloides [niger] lemosi* (south-central Colombia, from *rothschildi* in lower Andes of Argentina), *Synallaxis [azarae] elegantior* (Andean northern Colombia to Peru, from *frontalis* in eastern Brazil).

Sub-Andean Bolivia.—*Upucerthia [certhioides] harterti* (from *certhioides* in chaco).

Chile, or Chile and Patagonia.—*Nothura [perdicaria] perdicaria* (central Chile, from *cinerascens* in the subtropical deciduous forest of the eastern Andean slopes, fig. 14), *Glaucidium [brasilianum] nanum* (central Chile to southern Patagonia, from *brasilianum* in northern Chile and the eastern slopes of the Andes of northern

Argentina, fig. 30), *Picoides [mixtus] lignarius* (disjuncts in central Chile southward, and in mountain-valleys of Bolivia; from *mixtus* in the northern fringe of Patagonia, and in the lower Andean slopes of Bolivia, fig. 34), *Tachycineta [leucorrhoa] leucopyga* (Chile, Patagonia, from *leucorrhoa* in pampas and eastern Andean slopes).

Patagonia.—*Xolmis [cinerea] coronata* (northern Patagonia, adjacent Buenos Aires and La Pampa, from *cinerea* in northern Buenos Aires), *Mimus saturninus patagonicus* (central Patagonia to southern Buenos Aires, from *saturinus* in northern Buenos Aires, fig. 57).

Chaco and Adjacent Regions

Campos.—*Melanopareia [torquata] torquata* (to northeastern Bolivia and central Mato Grosso, from *maximiliani* in east-central Bolivia and the chaco), *Paroaria [gularis] baeri* (central campos, from *capitata* in chaco and Mesopotamian Argentina, fig. 67), *Sporophila [cinnamomea] cinnamomea* (three disjuncts, in south-central and north-central Mato Grosso, and in eastern Paraguay, from *hypochroma* in Corrientes, and central-eastern Bolivia), *Poospiza [melanoleuca] cinerea* (to western caatinga, from *melanoleuca* in chaco).

Subtropical dry forest.—*Knipolegus [cyanirostris] cabanisi* (to central Bolivia and southeastern Peru; from *cyanirostris* in eastern chaco), *Elaenia [mesoleuca] strepera* (from *mesoleuca* in eastern chaco, fig. 51).

West Indies and Middle America

West Indies.—*Sterna [albifrons] albifrons* (to islands off Venezuela, from northern Venezuela), *Columba [speciosa] squamosa* (to islands off Venezuela, from Venezuela).

Middle America. *Empidonax [albigularis] albigularis* (to western Panama, from *euleri* in northeastern Colombia).

DISCUSSION

Major disjunctions in range among species of the chaco can be categorized broadly as north-south disjunctions, east-west disjunctions, and northeast-southwest disjunctions (see fig. 80). Each category has many facets and is represented by many examples cited under the narrower categories listed above.

North-south disjunctions directly or indirectly

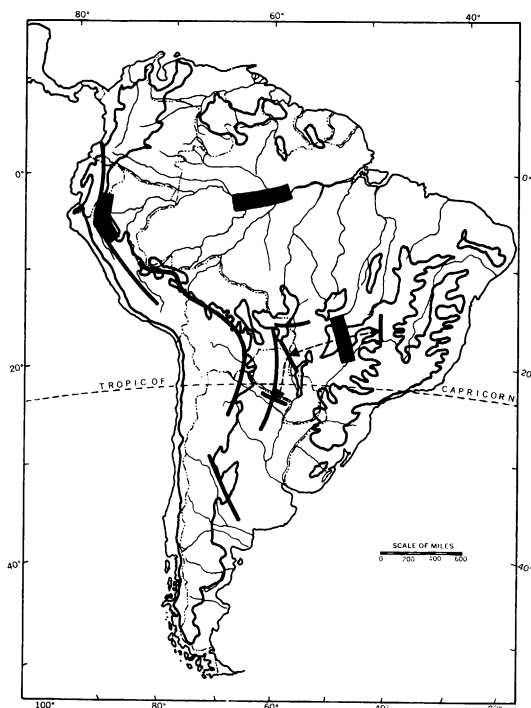


FIG. 80. Major range disjunctions in avian species inhabiting chaco. Black lines denote coinciding lines drawn from many species at approximate center of areas separating disjunct populations. These lines roughly indicate major barriers to avian distribution. Three broader lines denote most important barriers, and thinner lines, less important major barriers. These were determined roughly (and somewhat subjectively) by allowing greater weight for all allospecific disjunctions involving superspecies, and lesser weight for intra-specific disjunctions (see text).

involve Amazonia and include the northern South American disjuncts mainly separated from related southern populations by part or all of Amazonia, and disjunct populations within Amazonia, separated from more southern related populations. For chaco-dwelling species, disjunctions involving northern South America are the most numerous. This subcategory has 122 species showing conspecific northern disjuncts, about 60 percent of which have differentiated racially. Superspecies having disjunct allospecific pairs in the chaco region and in northern South America number 16. In contrast, far fewer chaco

species (54) have isolates in Amazonia itself, fewer of these have differentiated (43%), and only six allospecific pairs involve disjuncts within Amazonia. These major disjunctions are indicated in figure 80 by horizontal bars along the Amazon River and between Bolivia and adjacent Brazil. Of course divergent patterns are involved in each subcategory, but causes for these distributions probably are similar. Whatever the habitat in northern South America that is occupied by the particular disjunct population, the Amazonian forest generally may be regarded as a barrier interposed between it and its related population to the south. The distribution of such species of course may reflect a past connection by means of former favorable habitat either across Amazonia (e.g., savanna and edge corridors, Haffer, 1969), around Amazonia coastally to the east, or along the Andes to the west. Disjuncts within Amazonia are of several types, and different factors undoubtedly were involved in their history and evolution. Some isolates are savanna forms which cling to existence in Amazonian pockets of such habitat (e.g., *Colaptes campestris*, fig. 36, and *Ammodramus humeralis*, fig. 76), and others are Amazonian forest-dwelling forms that presumably have diverged in habitat preference from their related populations to the south.

East-west disjunctions include three basic patterns (fig. 80). These are west coastal-eastern lowland disjunctions (Andean barrier), Andean highland and/or Patagonian-eastern lowland disjunctions (Andean subtropical forest barrier), and trans-chaco disjunctions, in which the dry central chaco is the barrier. These disjunctions involve relatively few chaco species, but the number of allospecies is high and the proportion of species showing differentiation is rather high in at least the first two types of pattern. Of 45 species having disjunct populations west of the Andes 71 percent show racial differentiation, and 11 more allospecies represent superspecies the allospecies of which are so disjunct. Only 24 species are disjunct between the lowlands (chaco, chaco-pampas) and the Andes or Patagonia, but 71 percent show racial differentiation, and there are 13 allospecific pairs also exhibiting such a disjunct pattern. Data relating to these patterns suggest that species able to pass through or around the barrier, if it existed when they

assumed their ranges to either side of it, have tended to differentiate, perhaps rapidly, thus reflecting both the efficacy of the barrier and the distinctly different environments to which the freshly disjunct populations adapted. In contrast, the chaco itself is a weaker barrier and habitats at its western and eastern extremes perhaps are less markedly different, as indicated by the lesser proportion of disjuncts that have differentiated (35 percent of 14 species), and by the few (only two) allospecific pairs involved.

Northeast-southwest disjunctions (fig. 80) involve a gradient of separations. From the northeast to southwest these are: caatinga versus campo-chaco; eastern and southern Brazil generally versus campo edge and chaco; campo versus chaco, northern chaco versus southern chaco; chaco versus pampas and chaco-scrub (not indicated in fig. 80); and, as an extension of the gradient, chaco and pampas versus Chile and Patagonia (discussed as an east-west disjunction, see above). The total number of species involved in all but the last of these groups of disjunctions is 45, of which 53 percent have differentiated (mostly in the caatinga region). There are 14 allospecific pairs involved in these areas, and again most of the disjunct allospecies occur generally or restrictedly in the caatinga region.

Disjunctions associated with greater differentiation and speciation (fig. 80) are those involving broad barriers (e.g., the campo region interposed between drier chaco and caatinga areas), strong barriers (e.g. the Andes Mountains between lowlands west and east of it), or both (e.g., the Amazonian forests between more open habitats north and south of it). Obviously chaco-inhabiting birds tend to include species tolerant of xeric and semi-open situations; certain barriers most strongly affect this array of species. Other nearby areas with different ecological attributes, such as forested southeastern Brazil and the pampas, support somewhat different avifaunas that are apt to be differently affected than chaco birds by the types of barriers restricting the latter. Doubtless the nature of the disjunctions and efficacy of the barriers will vary considerably, depending on the nature of the area treated and the particular avifauna involved. It will be interesting to compare the relative efficacy of barriers, and patterns of disjunction affecting birds inhabiting more or less

ecologically distinct areas in the general area of the chaco with results of this analysis.

ZONES OF AVIAN INTERACTION, AND NARROW RANGE DISJUNCTIONS

The geography of various types of avian interaction involving secondary contact between previously isolated populations, at or below the level of species, and those range disjunctions of less than 100 miles involving chaco-occurring species will now be discussed. Avian interactions include: massive or restricted contacts between parapatric conspecific or allospecific populations, whether or not involving hybridization; hybrid zone phenomena (Short, 1970) among conspecific populations; local, narrow, or broad zones of overlap and hybridization between allospecific populations; and, narrow sympatry among allospecific populations. The narrow range disjunctions may of course involve populations at all taxonomic levels between consubspecific populations and allospecific populations.

As in the previous section a list of the forms involved geographically follows. In this case the pairs of forms are under headings denoting the regions occupied by the isolates, or former isolates; the northern or western isolate in each case is mentioned before the southern or eastern isolate.

North-South Isolates, Probably Middle American-South American

Middle America-South America, meeting or approaching in Middle America.—*Butorides [virescens] virescens-striatus* (Panama), *Jacana [spinosa] spinosa-jacana* (Panama), *Campephilus [melanoleucos] guatemalensis-melanoleucos* (Panama), *Camptostoma [obsoletum] obsoletum-imberbe* (Costa Rica), *Geothlypis [aequinoctialis] poliocephala-aequinoctialis* (Panama).

Caribbean region-South America.—*Sterna [albifrons] albifrons-superciliaris* (Venezuelan coast), *Columba [speciosa] squamosa-speciosa* (Venezuelan coast), *Coccyzus [minor] minor-melocoryphus* (overlap coastal Venezuela, and coast of Guyana to Amazon mouth), *Elaenia [martinica] martinica-flavogaster* (Venezuelan coast).

Middle America, northwestern South America—Eastern and central lowland South America.—*Ciccaba [huhula] nigrolineata-huhula* (ap-

proach in east-central Colombia to Orinoco Valley, one hybrid in Colombia), *Cacicus [haemorrhous] uropygialis-haemorrhous* (approach closely in eastern Ecuador, more distantly in central to northeastern Colombia).

North America, Middle America, northern South America, sub-Andean South America—Lowland eastern and central South America.—*Piranga flava, flava* group-*lutea* group, approaching closely in the southern Venezuela-Guyana region, and in central Bolivia.

North-South Isolates within South America

Northern South America—Northern to south-central South America (sub-Andean in north).—*Thlypopsis [sordida] fulviceps-sordida* (contact over 200 miles in northeastern Venezuela, fig. 63).

Northern South America—Amazonia and South-central South America.—*Icterus [cayanensis] chrysocephalus-cayanensis* (less than 100 miles apart from eastern Peru to Surinam, with contact and hybridization in upper Amazonian Brazil, and in Surinam-French Guiana, fig. 58).

South America north of the lower Amazon River, and south of it.—*Polyborus plancus, cheriway* group-*plancus* group (lower Amazon River contact, hybridization occurs), *Crax [rubra] alector-fasciolata* (separated by lower Amazon River for 100 miles or more).

Northern South America and Amazonia—Sub-Andean and south-central South America.—*Colaptes [punctigula] punctigula-melanochloros* (approach within 100 miles from northern Bolivia to central Mato Grosso), *Thamnophilus [caerulescens] amazonicus-caerulescens* (allopatric, possibly partly parapatric between Peru, Mato Grosso and Maranhão, fig. 42), *Sturnella [militaris] militaris-superciliaris* (allopatric, ranges close and possibly meeting in the northern campo region).

Northern South America and Amazonia—Chaco region.—*Celeus [elegans] elegans-lugubris* (parapatric, sporadic hybridization in north-central Bolivia and western Mato Grosso), *Icterus cayanensis, cayanensis* group-*pyrrhopterus* (interbreed through “*periporphyrus*” in Bolivia, fig. 58).

Bolivia, campo, caatinga—Pampas, chaco scrub, southeastern Brazil.—*Furnarius rufus, badius* group-*rufus* group (intergrade narrowly across São Paulo and Paraná, broadly in the chaco through “*paraguayae*”).

Bolivia, campo, caatinga—Chaco, chaco scrub.

—*Phacellodomus [rufifrons] rufifrons-sibilatrix* (parapatric in western chaco, overlap in north-central chaco, fig. 40).

Eastern campo, caatinga, northeastern Brazil—Chaco, subtropical dry forest, northeastern Argentina.—*Icterus cayanensis, tibialis* group—*pyrrhopterus* (interbreed in northern Paraguay to southwestern Mato Grosso through “valencio-buenoi,” fig. 58).

Eastern campo, northeastern Brazil, northern southeastern Brazil—Western campo and southern southeastern Brazil to chaco, monte, pampas.—*Sicalis flaveola, brasiliensis-pelzelni* (intergrade from central Mato Grosso to eastern Paraná, fig. 72).

Campo—Chaco and pampas.—*Picoides mixtus, cancellatus* group—*mixtus* group (interbreed in southwestern Mato Grosso and along north-eastern Paraguay-Brazil border, fig. 34), *Lepidocolaptes angustirostris, bivittatus* group—*angustirostris* group (interbreed north-central Bolivia through Mato Grosso to western Paraná), *Suiriri [suiriri] affinis-suiriri* (approach or parapatric eastern Bolivia to northeastern Paraguay, fig. 52), *Poliophtila dumicola, berlepschi-dumicola* group (interbreed in southwestern Mato Grosso).

Campo to eastern and southeastern Brazil—Chaco, pampas, sub-Andean Bolivia.—*Colaptes melanochloros, melanochloros* group—*melanolaimus* group (barely separated from central Bolivia to Paraguay River and south to southern Paraguay; hybrid zone southern Paraguay to coastal Rio Grande do Sul).

Campo—Pampas (Intra-chaco contact).—*Colaptes campestris, campestris-campestroides* (hybridize in central Paraguay, fig. 36).

Campo—Chaco (and parts of central Bolivia, but not pampas).—*Ara ararauna, ararauna-carinde* (uncertain contact along northern Paraguayan border), *Ara [maracana] maracana-auricollis* (overlap in southwestern Mato Grosso and adjacent Paraguay, fig. 26), *Nystalus maculatus, maculatus* group—*striaticeps* group (interbreed in west-central Mato Grosso, fig. 32), *Phacellodomus rufifrons, rufifrons* group—*sincipitalis* (interbreed in western to central Mato Grosso, fig. 40), *Melanopareia [torquata] torquata-maximiliani* (allopatric by 75 to 150 miles from eastern Bolivia to southwestern Mato Grosso), *Thryothorus [guarayanus] leucotis-guarayanus* (approach from northeastern Bolivia to southwestern Mato Grosso), *Sporophila [cinnamomea] hypochroma-cinnamomea* (Corrientes, southern Paraguay, possibly chaco also).

Northern South America to northern chaco—

Southern chaco, pampas, and Patagonia.—*Polyborus [chimachima] chimachima-chimango* (overlap eastern Formosa to northeastern Uruguayan border).

Chaco or pampas and chaco—Patagonia (also Andean monte).—*Eudromia [elegans] formosa-elegans* (within 50 miles or less in southwestern chaco, fig. 17), *Thripophaga [pyrrholeuca] baeripyrrholeuca* (parapatric or overlapping Mendoza to southern Buenos Aires), *Carduelis [magellanica] magellanica-barbata* (allopatric, approaching in northern Chile, and in south-central Andean Argentina, fig. 79).

Lowland Bolivia—Eastern and south-central (western and northern in one) South America.—*Pyrrhura [frontalis] devillei-frontalis* (hybridize in northern Paraguay; *frontalis* is southeastern Brazilian, fig. 28), *Sporophila leucoptera, leucoptera* group—*bicolor* (interbreed in Santa Cruz), *Carduelis magellanica, magellanica* group—*santacruzicae* (contact probable in south-central Bolivia, fig. 79).

West-East Isolates in South America

Andean uplands—Eastern lowlands.—*Nothura [maculosa] darwini-maculosa* (varying overlap and separation, Salta to Rio Negro, Argentina, fig. 16), *Buteo [albicaudatus] polyosoma-albicaudatus* (contact in Sierra de Córdoba, and in southern Buenos Aires), *Vanellus [chilensis] resplendens-chilensis* (approach in southern Colombia, and northern Chile, fig. 21), *Gallinago [gallinago] andina-gallinago* (approach along Andean slopes, Peru to Argentina), *Columba maculosa, albipennis-maculosa* (separate, possibly in contact in valleys of south-central Bolivia), *Elaenia [albiceps] albiceps-parvirostris* (probably meet in lower Andes of Bolivia and northern Argentina), *Mimus [triurus] dorsalis-triurus* (approach in Andean slopes of Bolivia and northern Argentina), *Thraupis bonariensis, darwini-bonariensis* group (approach in northwestern Bolivia).

Andean slopes—Eastern lowlands.—*Leptotila [verreauxi] megalura-verreauxi* (approach in southern Bolivia and Salta), *Picoides [mixtus] lignarius-mixtus* (approach in southern Bolivia, fig. 34), *Synallaxis [azarae] azarae-frontalis* (approach in west-central Bolivia), *Thamnophilus caerulescens, aspersiventer* group—*caerulescens* (including *gilvigaster, dinellii*, fig. 42) group (interbreed in central Bolivia), *Cacicus [chrysopterus] leucorhamphus-chrysopterus* (approach in central Bolivia).

Subtropical dry forest of western Argentina and Bolivia—Chaco.—*Picumnus* [*cirratus*] *dorbygnianus-cirratus* (contact, possible overlap in Salta, adjacent Bolivia, fig. 33), *Veniliornis* [*passerinus*] *frontalis-passerinus* (close approach in western Santa Cruz), *Pseudocolopteryx* [*acutipennis*] *dinellianus-acutipennis* (overlap in Tucumán), *Serpophaga subcristata*, *munda-subcristata* group (overlap as morphs from south-western chaco to La Pampa, fig. 50).

Chaco—Southeastern Brazil.—*Aburria* [*pipile*] *pipile-jacutinga* (close approach in central eastern Paraguay), *Strix rufipes*-*S. hylophila* (closely related, possibly a superspecies, close approach in eastern Formosa and adjacent western Paraguay, fig. 31), *Celeus* [*elegans*] *lugubris-flavescens* (approach closely in eastern Paraguay), *Dryocopus* [*pileatus*] *schulzi-lineatus* (approach closely along the Paraguay River, possibly hybridize in eastern Chaco Province, fig. 37), *Dendrocolaptes* [*picumnus*] *picumnus-platyrostris* (approach along Paraguay River, Mato Grosso to southern Paraguay), *Cyanocorax* [*caeruleus*] *cyanomelas-caeruleus* (approach in eastern Corrientes and eastern Paraguay, fig. 55), *Embernagra platensis olivascens-platensis* (intergrade from eastern Formosa to La Pampa, fig. 77).

Chaco, campo (and northward in some)—Southeastern Brazil.—*Leptotila verreauxi chrysauchenia-decipiens* group (intergrade along Parana and Upper Parana rivers and east to Rio de Janeiro), *Dryocopus lineatus*, *lineatus* group-*erythroptus* (interbreed as morphs from Paraguay River to Rio de Janeiro, fig. 37), *Campylorhamphus* [*trochilirostris*] *trochilirostris-falcularius* (approach from central São Paulo S and W to Corrientes, fig. 38), *Myiarchus swainsoni*, *pelzelni* group-*swainsoni* (interbreed eastern chaco and western Mesopotamia to coastal Brazil), *Contopus cinereus*, *brachytarsus* group-*cinereus* (interbreed from eastern Paraguay to Bahía, fig. 47), *Tachyphonus* [*rufus*] *rufus-coronatus* (overlap southeastern Mato Grosso to Misiones, fig. 62).

Chaco, pampas—Southeastern Brazil.—*Saltator* [*aurantiiostris*] *aurantiiostris-maxilloso* (interbreed to some extent in eastern Corrientes and adjacent Paraguay, and Rio Grande do Sul, fig. 66).

Chaco, campo—Coastal eastern Brazil.—*Crax* [*rubra*] *fasciolata-blumenbachii* (approach in Brazilian highlands), *Thryothorus* [*guarayanus*] -*T. longirostris* (close relatives, barely overlapping in Pernambuco to Piauí, then separate through Brazilian highlands), *Hemithraupis* [*guira*] *guira-*

ruficapilla (contact and some hybridization, and approaching inland from Paraná to Bahía).

Isolated Cases and Complicated Patterns

Lone instances, simple pattern.—*Aburria pipile*, *pipile* group-*cujubi* group (northern, sub-Andean, and chaco *pipile* group approaches lower Amazon and eastern Amazonian *cujubi* group from the south, in north-central Mato Grosso), *Thamnophilus caerulescens dinelli* and *gilviger* group-*caerulescens* group (interbreed in eastern Paraguay, and polymorphic from Corrientes to São Paulo thus with an intra-south-eastern Brazil contact, fig. 42), *Thlypopsis* [*sordida*] *inornata-sordida* (Marañón Valley *inornata* closely approaches widespread *sordida* in east-central Peru, fig. 63), *Saltator* [*coerulescens*] *coerulescens-similis* (Middle America to chaco and caatinga *coerulescens* hybridizes with south-eastern Brazilian *similis* from Mato Grosso to Uruguay, and the two approach or are separated from Mato Grosso to the caatinga, fig. 65), *Pheucticus* [*chrysopeplus*] *chrysogaster-aureoventris* (Andean *chrysogaster* approaches or meets sub-Andean and chaco edge *aureoventris* in two areas between southern Colombia and Peru), *Carduelis magellanica*, *magellanica* group-*olivacea* (the Andean and south-central South American *magellanica* group approaches and probably meets sub-Andean *olivacea* between Peru and Bolivia, fig. 79).

Complicated situations involving disjunct populations (refer to systematic accounts for discussion of ranges).—*Rallus* [*nigricans*] *sanguinolentus-nigricans* (overlap in eastern Paraguay, Rio de Janeiro; approach elsewhere), *Forpus* [*passerinus*] *xanthopterygius-passerinus* (approach closely in central Amazon Valley), *Anthracocorax* [*nigricollis*] *nigricollis-prevostii* (overlap in Venezuela), *Piculus* [*chrysochloros*] *chrysochloros-aurulentus* (approach over area from Corrientes to São Paulo, close approach in Rio de Janeiro), *Pyriglena* [*leucoptera*] *leucnota-leucoptera* (approach in Mato Grosso, also in northeastern Brazil), *Myiophobus* [*fasciatus*] *fasciatus-cryptoxanthus* (approach closely in eastern Peru), *Stigmatura* [*budytoides*] *budytoides-napensis* (overlap in part of caatinga, fig. 49), *Progne* [*subis*] *modesta-chalybea* (overlap in northwestern Peru and adjacent Ecuador, and in southern chaco to Río de la Plata, fig. 54), *Cyanocorax* [*chrysops*] *chrysops-cyanopogon* (approach closely in Paraguay to São Paulo, and

also in Pernambuco, fig. 56), *Thraupis* [*sayaca*] *sayaca-episcopus* (contact or likely contact occurs, or they approach each other closely in Venezuela, in northern Bolivia, and in Maranhão, fig. 61), *Coryphospingus* [*cucullatus*] *cucullatus-pileatus* (more or less closely approach in São Paulo and Minas Gerais, fig. 74), *Ammodramus* [*humeralis*] *aurifrons-humeralis* (overlap in llanos, in lower Amazon Valley, and in northern Bolivia, fig. 76), *Emberizoides* [*herbicola*] *herbicola-duidae* (widespread *herbicola* encircles montane *duidae*, with no contact but close approach).

DISCUSSION

The zones of interaction, parapatry, and zones between narrowly disjunct allospecies or well-differentiated subspecies or subspecies groups indicate present or former disjunctions in range that have persisted sufficiently long to permit differentiation of the forms involved. By no means do all of these contacts and disjunctions mark the actual areas in which the pairs of forms originally were separated. Contact zones, for example, are areas of strong interaction, either involving competition and enhancement of reproductive isolation (allospecies), or interbreeding and selective filtering of genes across a broader or narrower hybrid zone (conspecific populations). With the give and take associated with interplay of the various selective forces, these contact zones can be expected to shift gradually, and thus the zones of today may be somewhat removed from the original point of contact of the populations involved. Likewise, present narrow disjunctions may not mark the original area in which the disjunct forms were separated initially. The disjunction may have been much greater in the past, in some cases, and one or the other of a pair of disjunct forms subsequently may have expanded its range, narrowing the disjunction, while the other form may have maintained a static distribution. Thus, the present location of the disjunction may be skewed to one side or another of the original zone of separation of these populations. Nevertheless, most of the contact zones and narrow disjunctions can be expected to indicate reasonably well the approximate location of past barriers.

I have plotted the ranges of the taxa listed above. Actual zones of contact between allospecies, or other closely related species were marked. Zones of hybridization also were noted, and the approximate centers of these zones were marked. For narrow range disjunctions, I plotted the approximate center of the zone of separation of the taxa involved, and marked these. Wherever these various markings roughly coincided, I merged the lines for the distance over which they coincided. In figure 81 I have located these lines of coincidence where they involve three or more pairs of taxa. The approximation to these lines for various pairs is within 100 miles of the lines

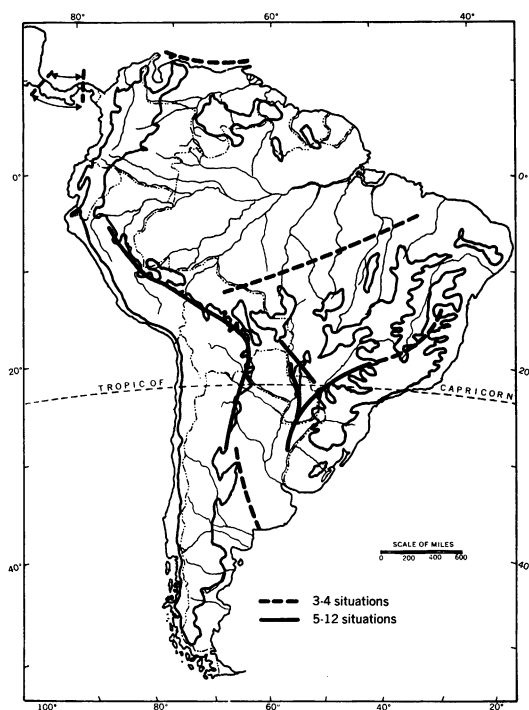


FIG. 81. Narrow range disjunctions, zones of hybridization, and other zones of avian interaction involving chaco birds (see text). Lines shown here mark coincidence of centers of such zones or areas of disjunction for various species, wherever they fall within 100 miles of center of lines shown. They are based on 70 interactions or contacts, and 28 narrow disjunctions (see text). These zones of interaction should be compared with barriers indicated in figure 80.

on the map. Other, similar patterns falling outside these borders were not included. The figure then highlights generally the main zones of interaction, parapatry, and narrow disjunctions.

Analysis of the 70 interactions and contacts, and the 28 narrow disjunctions indicates that chaco-dwelling species are most apt to have well-differentiated isolates or former isolates in southeastern Brazil, in the campo-caatinga region (with or without occurrence also in southeastern Brazil) and in the Andean region (fig. 81). These areas are of course adjacent to the chaco region, and have been accessible to but also isolated periodically from the chaco. Grassland is apt to have been the major isolating factor creating a barrier to the east of the chaco, enhanced by a water barrier when sea level was higher. The number of pairs of taxa involved in the Andean region is perhaps surprising, but the rather harsh climatic extremes in the chaco have at times apparently favored brushland and scrub species able to endure Andean (and sub-Andean) climates, and barriers (subtropical forest, at times perhaps humid) have permitted isolation and differentiation. Some of the Andean representatives or interacting or disjunct pairs also inhabit Patagonia. In contrast, there are many fewer isolates and former isolates in the nearby Amazonian region, and in the adjacent pampas, both of which show characteristics (respectively wet forest, grassland) differing markedly from those of the chaco.

The coincidence of the distributional patterns at the eastern chaco border is remarkable (fig. 81). Chaco species or forms of the pairs considered tend to extend into Corrientes, and the southwestern corner of eastern Paraguay, rather than stop at the Paraguay-Parana rivers. This provides avifaunal corroboration of the chaco limits in this region, suggested by vegetational studies (discussed above), and, with far fewer data, by Short (1971b).

The relatively few interactive zones between South and Middle America reflect the occurrence of widespread South American species, usually of edges, open (xeric) country or aquatic situations, that have undergone isolation from related Middle American populations. Widespread forest species not occurring in the chaco are apt to show more differentiation from related Middle American forest populations, in view of the history of

northwestern South America and adjacent Panama (Haffer, 1967).

Comparing patterns of major range disjunction (fig. 80) with those of interactions and narrow range disjunctions (fig. 81), certain similarities and differences are apparent. Major range disjunctions of course indicate presently effective barriers to distribution of the forms involved. Thus, there is a major barrier between west coastal Peru and Ecuador, and the eastern Andean lowlands (fig. 80) that is not apparent in the interactive zone and minor disjunction pattern (fig. 81), simply because these areas are isolated and are unconnected by ecologically suitable habitat, hence a close approach in range or actual contact is not possible. Amazonian forests are a barrier widely separating a number of disjunct pairs, but are not a contact zone; rather pairs involving one element from Amazonia make contact (fig. 81) or show narrow disjunctions at the southern edge of Amazonia. Major disjunctions generally are within the central portion of a presumed barrier (fig. 80), often an unfavorable ecological formation, but zones of contact and narrow disjunctions occur generally between different ecological formations or near a border of such a formation (fig. 81).

The zones of avian interaction and narrow disjunctions indicate other centers of differentiation of chaco-occurring birds than the chaco region and its surroundings. These other centers, for the nearly 25 percent of chaco-dwelling birds that show such interactions and disjunctions, as noted above, are the campo-caatinga region, forested southeastern Brazil, the Andean-sub-Andean region, and to a lesser extent, Patagonia and Amazonia. The low endemicity of the chaco avifauna, and other factors discussed above make it likely that, among the pairs of forms engaged in interactions or narrow disjunctions, the chaco-dwelling elements of the pairs did not evolve in the chaco, but in adjacent areas to one side or another of the chaco (although probably including parts of the present-day chaco). Most closely tied distributionally to the chaco among the 98 pairs of forms listed above are *Eudromia [elegans] formosa* (fig. 17), *Strix rufipes* (fig. 31), *Celeus [elegans] lugubris*, *Dryocopus [pileatus] schulzi* (fig. 37), *Melanopareia [torquata] maximiliani*, and *Phacellodomus [rufifrons] sibilatrix* (fig. 40). Only these species and perhaps a

few others probably have had their speciation affected primarily by ecological developments within the chaco. The other species of pairs involved with these species in interactions or narrow disjunctions exhibit a variety of patterns, so each pair has had a distinctive history.

A partial breakdown of chaco species showing interactions or narrow disjunctions is of interest in comparison with polytypic chaco species and with totals for all chaco species in the same categories. Of the 409 chaco species, 53 percent are nonpasserines, a proportion almost matched by the nonpasserine 51 percent of 276 chaco species exhibiting polytypy. In the categories of chaco species, and of polytypic chaco species the following groups of birds respectively comprise these proportions: suboscine birds, 24 and 26 percent; oscines of Old World origin, 5 and 5 percent; and, nine-primaried oscines (including cardueline species), 17 and 18 percent. The 98 situations involving avian interactions and narrow range disjunctions include 41 nonpasserine birds (42 percent), 23 suboscines (23 percent), seven oscines of Old World origin (7 percent), and 27 nine-primaried oscines (28 percent). The differences in proportions from the chaco totals and the chaco polymorphic species are mainly in the diminished nonpasserines and increased nine-primaried oscines involved in these interactions and narrow disjunctions. The differences of values between situations of interactions and narrow disjunctions and proportions of chaco species in these categories is significant (Chi-Square test, $P = 0.05$ to 0.01), and between those situations and proportions of polytypic chaco species approaches significance ($P = 0.20$ to 0.05). However, they are rendered highly significant when one considers that the species involved in the interactions and narrow disjunctions are included within both the chaco species, and chaco polytypic species; their exclusion from these groups would render the differences much greater. It will be interesting to see if analyses of other South American avifaunas corroborate the apparently greater speciation of the nine-primaried oscine group reflected by these data.

ZONES OF PRIMARY INTERGRADATION AMONG CHACO BIRDS

The approximate racial borders of the subspecies of polytypic chaco birds were plotted on a

series of maps. Examination of these rough boundaries with the use of a transparent overlay allowed the determination of coinciding patterns. Such patterns are considered to coincide when the racial borders of two (or more) species are parallel for 50 miles or more and when the parallel borders are less than 50 miles apart. With these finite limits it was found that parts (often only small) of the racial borders of about two-thirds of the 276 polytypic chaco species showed coincidence.

In figure 82 I have plotted on a map the coincidental racial borders involving several to many chaco species. Morphological characters of numbers of chaco species tend to shift their

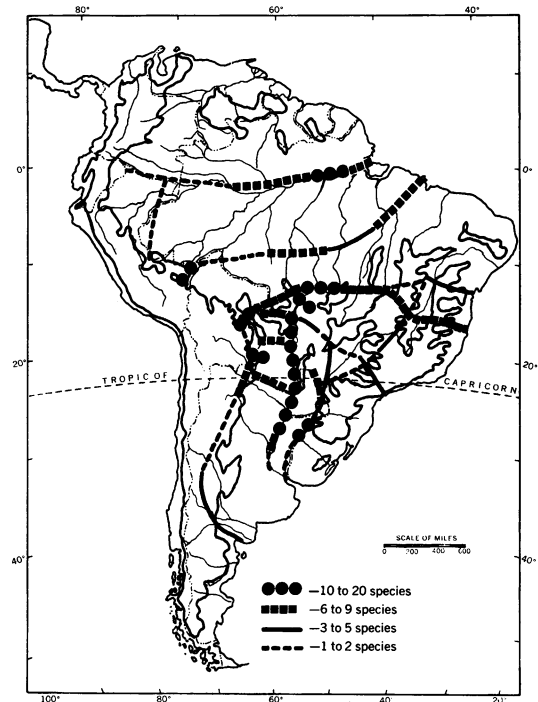


FIG. 82. Zones of primary intergradation among birds of chaco. These lines depict approximately coincidental centers of areas of intergradation among the 276 polytypic chaco species. Coincidence was noted whenever racial borders in two or more species were less than 50 miles apart and extended parallel to one another for more than 50 miles. The coincidences summarized here affect about two-thirds of 276 polytypic species. Compare with figures 80 and 81. See text.

expression clinally (no attempt is made here to define the nature of the clines, whether step-clines or otherwise, or to assess the relative significance of the observed shifts in terms of the number of morphological characters undergoing shifts in diverse species) in certain more or less well-defined areas. It is clear that well-defined north-south gradients shift in the Amazon Valley region, between Amazonia and the cerrado-campo region, and in the southern campo. These shifts are marked in the lower Amazon Valley (more species are involved), and along the base of the Andes Mountains. Major east-west shifts occur along the Paraguay River, and to some extent along the Uruguay and Upper Parana rivers, and at the eastern base of the Andes Mountains in Bolivia and northern Argentina.

That these morphoclines relate to environmental shifts is likely, but confirmation requires correlative studies. To some extent, as in the Amazon Valley and along the Paraguay River, clines may be stepped, enhanced, or "focused" on these natural gaps in avian distribution. These areas of shift in morphoclines, and some of the others shown on the map (fig. 82) may reflect also the past occurrence of distributional barriers, still detectable by virtue of the clines (see the sections on avian interaction, and major disjunctions in range).

Polytypic species number 276 of the 409 chaco species. Of the 276 species, apparently significant size differences among races have been reported for 81 species ("significance" was not established, but the term here infers that I have ignored differences reported in the literature as "slight"). The size differences are mentioned here because of some apparent correlation with Bergmann's Ecogeographic Rule, suggesting environmental effects on clinal variation in at least some cases of primary intergradation. Of the 81 species, 69 (40 passerine species, 29 non-passerine species) show races characterized by larger size (usually inferred from wing length data) occurring south of races showing smaller size. This observation is in accord with Bergmann's Rule (larger forms in cooler regions, toward the poles, smaller forms in warmer, more tropical region). Not all of these species involve contiguous races and continuous clines (some races are disjunct). Three of the 29 cases in non-

passerine birds involve two southern races, in the eastern chaco (and eastward), and in the western chaco (and westward), both larger than races to the north. Additionally, in five superspecies, the southern allopecies of a pair or of several allopecies distributed also in the tropics are larger than their northern relatives.

Twelve species show apparent discordance with Bergmann's Rule, although in three of these cases the northern, larger races are not tropical but Andean, hence do not relate to this phenomenon (whether their Andean habitat is "cooler" than the environments of more southern races is uncertain). The nine species showing smaller size southerly are the nonpasserine *Anas versicolor*, *Ortalis canicollis*, *Parabuteo unicinctus*, *Dromococcyx pavoninus*, *Strix rufipes*, *Amazilia chionogaster*, and *Piculus chrysochloros*, and the passerines *Machetornis rixosus* and *Icterus cayanensis*. Additionally, in two superspecies, *Suiriri suiriri* and *Fulica atra*, the southern of the two adjacent allopecies (respectively *S. suiriri* and *F. leucoptera*) is smaller than its northern relative.

Thus, about seven times as many chaco species show concordance with Bergmann's Rule as show discordance, suggesting the strong (direct or indirect) influence of environmental factors, in this case temperature and associated parameters, on the variation in these species.

ORIGINS OF THE CHACO AVIFAUNA

What can we conclude about the origins of the "chaco avifauna"? We have seen that this avifauna is at best only mildly distinctive, for most of its species extend well beyond the chaco and but a few are restricted or nearly restricted to it. Widespread species, whatever their origin, tend to occur wherever habitat is favorable. It is doubtful that any widespread South American species originated within the chaco, but rather such forms have invaded from elsewhere. It is impossible to establish where they arose, except that most of them undoubtedly entered from the north and northeast.

If we exclude the cosmopolitan South American species, then those of somewhat or very restricted distribution do exhibit patterns suggesting that chaco birds largely are derived from arid scrub, semi-open country, and forest edges

situated to the north (including northern South America) and east of the chaco. Data from major avian disjunctions, and from narrow disjunctions and zones of interaction reinforce this. Evidently xeric habitats generally have been available for a considerable period of time, although their precise locations and interconnections have shifted greatly and undergone fluctuations. As an example, the caatinga, which shows considerably greater endemism than the chaco, both botanically and zoologically, has varied in its extent and location. Its direct connection with the chaco at some time in the past must I think be assumed on the bases of vegetational and certain avifaunal (e.g., *Nothura boraquira*, fig. 15) similarities. Its separation(s) from the chaco has allowed some differentiation of once continuously distributed, xeric-adapted forms isolated in each area. On the other hand, many partially xeric-adapted forms not occupying all of the caatinga or perhaps the chaco, but tolerant of semi-open, less arid country found in the campo region, have retained (or even expanded) their distribution between the caatinga and chaco through the intervening campo-cerrado region.

Distinctive elements of the chaco avifauna are derived from other sources, of course. For example, the chaco has a tinamou fauna of 10 species, two more than the caatinga. Two of its major tinamou genera, *Nothura* and *Eudromia*, respectively are Andean-Patagonian-chaco-pampan, and chaco-pampan in distribution. Of the four chaco species of *Nothura* (figs. 14 to 16), only two reach the caatinga, which lacks additional species of this genus. *Eudromia* (fig. 17) does not reach the caatinga. Neither *Nothura* nor *Eudromia* is found within or north of Amazonia. Most chaco tinamous thus appear derived from the south or west. Interestingly, two of the three chaco species of *Crypturellus* (fig. 12) also occur in the caatinga, which has five species (of the total of eight caatinga tinamous) of this genus. *Cryp-*

turellus essentially is a tropical forest group numbering some 20 species (Meyer de Schauensee, 1966), and these extend barely beyond the chaco to the pampas edge and the lower Andean slopes (not the plateaus). The likely origin of *Crypturellus* species in the chaco is the caatinga and surrounding regions north and east of the chaco. Thus, various elements of one family or subfamily, and even of a genus, may show divergent origins.

Of all the xeric woodland formations in South America, the chaco probably has undergone the greatest shifts in its borders. It also is large, and is centrally located on the continent, affording access and transconnection of xeric-adapted forms from the west and northwest (scrub deserts of Andean valleys, Peruvian coastal and inland scrub areas), from the south (Patagonian steppe scrublands, and chaco scrub), and from the northeast (caatinga, and probably through its connections, with arid zones in northern South America). These factors relate to the lack of distinctiveness of the chaco avifauna, but they also emphasize the importance of the chaco in furthering the distribution, and ultimate isolation elsewhere, of many forest edge and scrub woodland species.

The origins of the chaco avifauna are diverse and extrinsic. Analysis of distribution patterns within avian families, and genera, based on knowledge not yet at our disposal, will be necessary before we can explain fully the origins of the chaco's birds. The results of such studies should corroborate the general patterns indicated by the taxonomic and distributional analysis presented herein. Other avifaunas must be investigated to place the present study in perspective. I hope that I have encouraged colleagues to treat other South American avifaunas, and to conduct zoogeographic analyses of families and genera of Neotropical birds, so vital to our understanding of avian zoogeography of South America.

LITERATURE CITED

- Amadon, D.
1966. The superspecies concept. *Syst. Zool.*, vol. 15, pp. 245-249.
- Auer, V.
1970. The Pleistocene of Fuego-Patagonia. Part V. Quarternary problems of southern South America. *Ann. Acad. Sci. Fennicae*, ser. A, III, geol.-geogr., no. 100, pp. 1-194.
- Bakker, J. P.
1968. Die Flussterrassen Surinams als Hinweis auf etwas trockenere Klimate

- während der Quartären Eiszeiten. *Acta Geogr. Debrecin*, vol. 7, pp. 9-17.
- Bigarella, J. J., and A. N. Ab' Sáber
1964. Palaeogeographische und Palaeoklimatische Aspekte des Kaenozoikums in Suedbrasilien. *Zeitschr. Geomorph.*, vol. 8, pp. 286-312.
- Bigarella, J. J., M. R. Mousinho, and J. X. Da Silva
1965. Considerações a respeito da evolução dos vertentes. *Bol. Paranaense Geogr.*, nos. 16-17, pp. 85-116.
- Blake, E. R.
1968. Family Icteridae. *In* Check-list of birds of the world, vol. XIV. Cambridge, Mus. Comp. Zool., pp. 138-202.
- Bó, N. A.
1969. Acerca de la afinidad de dos formas de *Serpophaga* (Aves, Tyrannidae). *Neotropicalica*, vol. 15, pp. 54-58.
- Bock, W. J.
1958. A generic review of the plovers (Charadriinae, Aves). *Amer. Mus. Novitates*, no. 1779, pp. 1-49.
- Brodkorb, P.
1963. Catalogue of fossil birds. Pt. 1. *Bull. Florida State Mus.*, vol. 7, pp. 179-293.
1964. Catalogue of fossil birds. Pt. 2 (Anseriformes through Galliformes). *Ibid.*, vol. 8, pp. 195-335.
1967. Catalogue of fossil birds. Pt. 3 (Ralliformes, Ichthyornithiformes, Charadriiformes). *Ibid.*, vol. 11, pp. 99-220.
- Brown, L., and D. Amadon
1968. Eagles, hawks and falcons of the world. New York, McGraw-Hill Book Co., pp. 1-945 (2 vols.).
- Conover, B.
1950. A study of the spotted tinamous, genus *Nothura*. *Fieldiana (Zool.)*, vol. 31, pp. 339-362.
- Delacour, J., and D. Amadon
1973. Curassows and related birds. New York, *Amer. Mus. Nat. Hist.*, x + 247 pp.
- Eidt, R. C.
1968. The climatology of South America. *In* Biogeography and ecology of South America. *Monographiae Biologicae*, vol. 18, pp. 54-81.
- Eisenmann, E., and L. L. Short
[MS.] Systematics of the Neotropical emberizine genus *Emberizoides*.
- Fry, C. H.
1970. Ecological distribution of birds in north-eastern Mato Grosso State, Brazil. *Ann. Acad. brasiliense Cien.*, vol. 42, pp. 275-318.
- Goodwin, D.
1967. Pigeons and doves of the world. London, British Museum (Nat. Hist.), pp. 1-446.
- Gorham, J. R.
1973. The Paraguayan chaco and its rainfall. *In* Paraguay: ecological essays. Gainesville, Florida, Acad. Arts Sci. Amer., chap. 4, pp. 39-60.
- Groot, J. J., and C. R. Groot
1966. Pollen spectra from deep sea sediments as indicators of climatic changes in southern South America. *Marine Geol.*, vol. 4, pp. 525-537.
- Haffer, J.
1967. Speciation in Colombian forest birds west of the Andes. *Amer. Mus. Novitates*, no. 2294, pp. 1-57.
1969. Speciation in Amazonian forest birds. *Science*, vol. 165, pp. 131-137.
1970a. Art-Entstehung bei einigen Waldvögeln Amazoniens. *Jour. Ornith.*, vol. 111, pp. 285-331.
1970b. Geologic-climatic history and zoogeographic significance of the Uraba region in northwestern Colombia. *Caldasia*, vol. 10, pp. 603-636.
- Hall, B. P., and R. E. Moreau
1970. An atlas of speciation in African passerine birds. London, *Brit. Mus. (Nat. Hist.)*, publ. 680, xv + 423 pp.
- Haverschmidt, F.
1968. Birds of Surinam. Edinburgh and London, Oliver and Boyd. xxix + 445 pp.
- Hellmayr, C. E.
1935. Catalogue of birds of the Americas and the adjacent islands. Part 8. *Field Mus. Nat. Hist.*, publ. 347, zool. ser., vol. XIII, vi + 541 pp.
1937. Catalogue of birds of the Americas and the adjacent islands. Part 10. *Ibid.*, publ. 381, zool. ser., vol. XIII, v + 228 pp.
- Heuck, K.
1966. Die Wälder Südamerikas. Ökologie, Zusammensetzung und wirtschaftliche Bedeutung. *Vegetationsmonographien der einzelnen Grossräume*, vol. 2. Stuttgart, G. Fischer Verlag, xviii + 422 pp.
- Johnsgard, P. A.
1965. Handbook of waterfowl behavior. Ithaca, Cornell Univ. Press, xiv + 378 pp.
- Kahl, M. P.
1971. Social behavior and taxonomic relations of the storks. *Living Bird*, vol. 10, pp. 151-170.

- Laubmann, A.
 1930. Vögel. Wissenschaftliche Ergebnisse der Deutschen Gran-Chaco Expedition. Stuttgart, Strecker and Schröder, xv + 334 pp.
 1939. Die Vögel von Paraguay. Wissenschaftliche Ergebnisse der Deutschen Gran-Chaco Expedition. Vol. 1. Stuttgart, Strecker and Schröder, xv + 246 pp.
 1940. Same title. Vol. 2. Stuttgart, Strecker and Schröder, vi + 228 pp.
- Lowery, G. H., Jr., and L. L. Short
 1969. Un registro de *Sporophila caerulescens* del Chubut. Neotropica, vol. 15, p. 63.
- Lüders, R.
 1961. Bodenbildungen im Chaco Boreal von Paraguay als Zeugen des spät- und postglazialen Klimaablaufs. Geol. Jahrb., vol. 78, pp. 603-608.
- Mayr, E.
 1946. History of the North American bird fauna. Wilson Bull., vol. 58, pp. 3-41.
- Mayr, E., and L. L. Short
 1970. Species taxa of North American birds. A contribution to comparative systematics. Nuttall Ornith. Club, publ. 9, pp. 1-127.
- Meyer de Schauensee, R.
 1966. The species of birds of South America with their distribution. Philadelphia, Acad. Nat. Sci., xvii + 577 pp.
 1970. A guide to the birds of South America. Philadelphia, Acad. Nat. Sci., xiv + 470 pp.
- Mitchell, M. H.
 1957. Observations on the birds of south-eastern Brazil. Toronto, Univ. of Toronto Press, x + 258 pp.
- Moynihan, M.
 1959. A revision of the family Laridae (Aves). Amer. Mus. Novitates, no. 1928, pp. 1-42.
- Naumburg, E. M. B.
 1930. The birds of Matto Grosso, Brazil. Bull. Amer. Mus. Nat. Hist., vol. 60, pp. 1-432.
 1939. Studies of birds from eastern Brazil and Paraguay, based on a collection made by Emil Kaempfer. *Ibid.*, vol. 76, pp. 231-276.
- Olrog, C. C.
 1959. Tres nuevas subespecies de aves argentinas (Tinamiformes). Neotropica, vol. 5, pp. 39-44.
 1963. Lista y distribución de las aves argentinas. Op. Lilloana IX, pp. 1-377.
 1968. Las aves sudamericanas, una guía de campo. Vol. 1. Tucumán, Argentina, Inst. Miguel Lillo, Univ. Nac. Tucumán, pp. 1-507.
- Olson, S. L.
 1970. The relationships of *Porzana flavi-venter*. Auk, vol. 87, pp. 805-808.
- Parkes, K. C.
 1960. The Brown Cachálote [*sic*], *Pseudosei-sura lophotes*, in Bolivia. Auk, vol. 77, pp. 226-227.
- Paynter, R. A., Jr.
 1970. Subfamily Emberizinae. In Check-list of birds of the world, vol. XIII. Cambridge, Mus. Comp. Zool., pp. 3-214.
- Pinto, O. M.
 1944. Catálogo das aves do Brasil. Pt. 2. São Paulo, Publ. Depto. Zool., Sec. Agric., Industr., Comerc., xi + 700 pp.
- Putzer, H.
 1962. Geologie von Paraguay. Beiträge zur regionalen Geologie der Erde, vol. 2. Berlin, Borntraeger Gebr., xii + 183 pp.
- Schwartz, P.
 1972. *Micrastur gilvicollis*, a valid species sympatric with *M. ruficollis* in Amazonia. Condor, vol. 74, pp. 399-415.
- Short, L. L.
 1965. Hybridization in the flickers (*Colaptes*) of North America. Bull. Amer. Mus. Nat. Hist., vol. 129, pp. 307-428.
 1967. A review of the genera of grouse (Aves, Tetraoninae). Amer. Mus. Novitates, no. 2289, pp. 1-39.
 1968. Sympatry of red-breasted meadowlarks in Argentina and the taxonomy of meadowlarks (Aves: *Leistes*, *Pezites*, and *Sturnella*). *Ibid.*, no. 2349, pp. 1-40.
 1969a. Taxonomic aspects of avian hybridization. Auk, vol. 86, pp. 84-105.
 1969b. A new species of blackbird (*Agelaius*) from Peru. Occas. Papers Mus. Zool., Louisiana State Univ., no. 36, pp. 1-8.
 1969c. Relationships among some South American seedeaters (*Sporophila*), with a record of *S. hypochroma* for Argentina. Wilson Bull., vol. 81, pp. 216-219.
 1970. Notes on the habits of some Argentine and Peruvian woodpeckers (Aves, Picidae). Amer. Mus. Novitates, no. 2413, pp. 1-37.
 1971a. Systematics and behavior of some North American woodpeckers, genus *Picoides* (Aves). Bull. Amer. Mus. Nat. Hist., vol. 145, pp. 1-118.
 1971b. Aves nuevos o poco comunes de Corrientes, República Argentina. Rev. Mus.

- Argentino Cien. Nat. "Bernardino Rivadavia," zool., vol. 9, pp. 283-309.
- 1972a. Systematics and behavior of South American flickers (Aves, *Colaptes*). Bull. Amer. Mus. Nat. Hist., vol. 149, pp. 1-110.
- 1972b. Relationships among the four species of the superspecies *Celeus elegans* (Aves, Picidae). Amer. Mus. Novitates, no. 2487, pp. 1-26.
- Short, L. L., and W. J. Bock
1970. Correspondence. Auk, vol. 87, p. 209.
- Smith, E. T.
1960. Review of *Pionus maximiliani* (Kuhl). Fieldiana (zool.), vol. 39, pp. 379-385.
- Smith, W. J.
1966. Communication and relationships in the genus *Tyrannus*. Nuttall Ornith. Club, publ. 6, ix + 250 pp.
- Steinbacher, J.
1962. Beiträge zur Kenntnis der Vögel von Paraguay. Abhandl. Senckenbergischen Naturf. Gesell., no. 502, pp. 1-106.
1968. Weitere Beiträge über Vögel von Paraguay. Senckenbergiana Biol., vol. 49, pp. 317-365.
- Sutton, G. M.
1944. The kites of the genus *Ictinia*. Wilson Bull., vol. 56, pp. 3-8.
- Tower, W. S.
1918. The pampa of Argentina. Geogr. Rev., vol. 5, pp. 293-315.
- Vaurie, C.
1968. Taxonomy of the Cracidae (Aves). Bull. Amer. Mus. Nat. Hist., vol. 138, pp. 131-260.
1971. Classification of the ovenbirds (Furnariidae). London, H. F. and G. Witherby, Ltd., pp. 1-46.
- Vaz-Ferreira, R., and E. Gerzenstein
1961. Aves nuevas o poco conocidas de la República Oriental del Uruguay. Com. Zool. Mus. Hist. Nat. Montevideo, vol. 5, pp. 1-65.
- Vuilleumier, B. S.
1971. Pleistocene changes in the fauna and flora of South America. Science, vol. 173, pp. 771-780.
- Wetmore, A.
1926. Observations on the birds of Argentina, Paraguay, Uruguay and Chile. Bull. U. S. Natl. Mus., no. 133, pp. 1-448.
1965. The birds of the Republic of Panamá. Part 1. Tinamidae (tinamous) to Rynchopidae (skimmers). Smithsonian Misc. Coll., vol. 150 (pt. 1), iv + 483 pp.
1967. Further systematic notes on the avifauna of Panamá. Proc. Biol. Soc. Washington, vol. 80, pp. 229-242.
1968. The birds of the Republic of Panamá. Part 2. Columbidae (pigeons) to Picidae (woodpeckers). Smithsonian Misc. Coll., vol. 150 (pt. 2), v + 605 pp.
- Zimmer, J. T.
1947. Studies of Peruvian birds. No. 51. The genera *Chlorothraupis*, *Creurgops*, *Eucometis*, *Trichothraupis*, *Nemosia*, *Hemithraupis*, and *Thlypopsis*, with additional notes on *Piranga*. Amer. Mus. Novitates, no. 1345, pp. 1-23.
1949. Same title. No. 54. The families Catamblyrhynchidae and Parulidae. *Ibid.*, no. 1428, pp. 1-59.
1955. Same title. No. 66. The swallows (Hirundinidae). *Ibid.*, no. 1723, pp. 1-35.

