

## SOME ALLOPATRIC SPECIES PAIRS OF BIRDS IN NORTH-WESTERN COLOMBIA

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THE lowlands around the Gulf of Urabá, in extreme northwestern Colombia, connect the isthmus of Panamá with the mainland of South America. This densely forested area is today the meeting place of various Central and South American faunas (Haffer, 1967*a*, *b*). Many bird species have advanced into the Urabá region from the Amazonian basin, coming around the northern tip of the Andes and, in a lesser number, have extended their range southward from Central America. In the Urabá area some of these forms made contact with their strongly differentiated representatives of the Chocó region of western Colombia. These zones of contact reveal striking faunal discontinuities in a continuous forest environment.

At the present time the tropical lowland forests extend without interruption (not taking into consideration recent changes through the activity of man) from the base of the northern Andes in Colombia throughout Central America, covering mainly the Caribbean slope north to Mexico. This continuity of the forests, however, represents only a temporary stage in the vegetational history of these areas as suggested by the climatic changes which affected the northern part of the Neotropical Region during the Pleistocene and post-Pleistocene. Van der Hammen and Gonzalez (1960) and van der Hammen (1961) have shown, by analyzing the pollen contents of lake and bog deposits of the highlands of the Eastern Cordillera of Colombia, that the Pleistocene and Holocene climate of the northern Andes mountains was characterized by a succession of cold-wet and dry-warm phases. This succession closely correlates with the contemporaneous sequence of climatic events known from North America and Europe. In contrast to the situation in the highlands of tropical mountains, the surrounding lowlands probably were only weakly affected by the Pleistocene temperature changes (Mortensen, 1957; Wilhelmy, 1957). However, the variation of average rainfall and cloud cover during these climatic periods seems severely to have influenced the distribution of tropical lowland forests and non-forest vegetation. It is the author's view, explained in detail elsewhere (Haffer, 1967*a*), that during arid climatic phases the presently continuous lowland forest zone of northwestern South America and Central America was broken up into a number of forest refugia which have been named as follows: Caribbean Central American Refugia, Chiriquí Refuge, Chocó Refuge, and Nechí Refuge (Figure 1). Most probably, additional isolated forests often remained

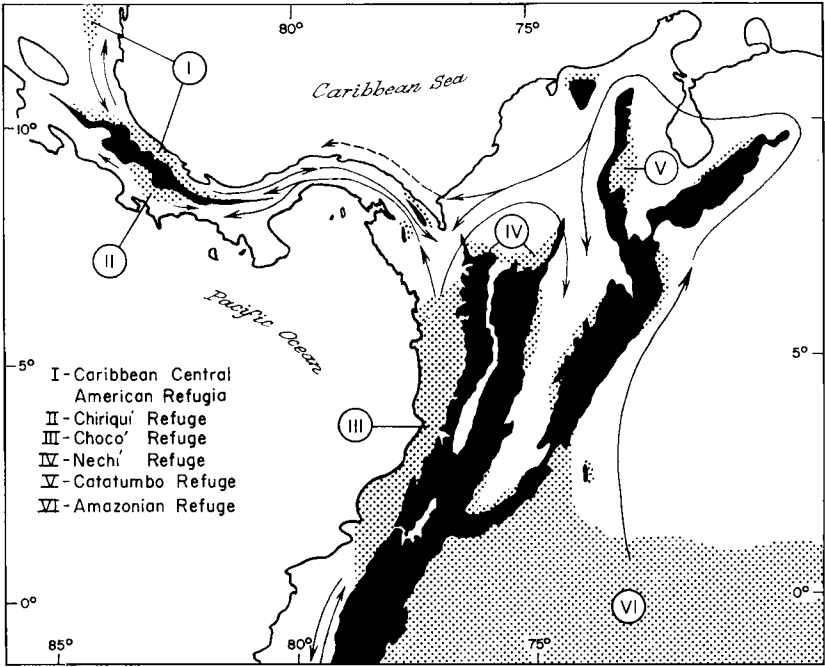


Figure 1. Presumed forest refugia in northwestern South America and southern Central America during Pleistocene and post-Pleistocene periods of drought. Elevations above 1,000 meters are in black; forests are stippled; arrows indicate advancing forest faunas during humid climatic phases. Other forest refugia probably existed in Central America north of the area shown.

also in the following areas: at the northern and northeastern base of the mountains of eastern Panamá; along the base of the mountains on both sides of the upper and middle Magdalena Valley of Colombia; at the northern base of the Sierra Nevada de Santa Marta near the Caribbean coast; and at the eastern base of the Perijá mountains of northeastern Colombia, etc. The last forest probably was rather extensive and may be named herewith the Catatumbo Refuge. (This refuge is named from the Rio Catatumbo which flows down the eastern slope of the Serranía de Perijá where the forest is broadest today.) East of the Andes remained the large Amazonian Refuge whose extent and shape also probably have changed repeatedly during the various climatic periods.

The isolated forests of the refugia rejoined, forming again a continuous forest zone, during humid climatic phases. Great numbers of Amazonian forest birds probably advanced through these continuous forests into northern and western Colombia and into Central America, coming around

TABLE 1  
SOME SPECIES PAIRS OF NORTHWESTERN COLOMBIA AND THEIR PRESUMED  
GEOGRAPHICAL ORIGIN<sup>1</sup>

<i>Crax rubra</i> (Ch)	<i>Crax alberti</i> (N)
<i>Aramides wolfi</i> (Ch)	<i>Aramides cajanea</i> (A)
<i>Pteroglossus (torquatus) sanguineus</i> (Ch)	<i>Pteroglossus torquatus</i> (C)
<i>Galbula (ruficauda) melanogenia</i> (Ch)	<i>Galbula ruficauda</i> (A)
<i>Formicarius nigricapillus</i> (Ch)	<i>Formicarius analis</i> (A)
<i>Manacus (manacus) vitellinus</i> (Ch)	<i>Manacus manacus</i> (A)
<i>Pipra mentalis</i> (Ch)	<i>Pipra erythrocephala</i> (A)
<i>Rhynchocyclus brevirostris</i> (Ch?)	<i>Rhynchocyclus olivaceus</i> (A)
<i>Cyanerpes lucidus</i> (C)	<i>Cyanerpes caeruleus</i> (A)
<i>Gymnostinops cassini</i> (Ch)	<i>Gymnostinops guatimozinus</i> (N)

<sup>1</sup> The presumed geographical origin of these forms is indicated in parentheses: Ch = Chocó Refuge, A = Amazonian Refuge, N = Nechí Refuge, C = Central American Refuge (see text and Figure 1).

the northern tip of the Andes and following the lowlands along the Caribbean coast. Upon the return of more arid conditions, many of the trans-Andean (i.e., west of the Andes) forest birds survived in the forest refugia described above. These various refuge populations north and west of the Andes would have been modified in isolation from their Amazonian parental populations and from one another. They must have reached many different levels in the speciation process before, in some cases, they made contact again during a later humid phase with one of their representatives which also would have been evolving in some other forest refuge. In my view, these processes of isolation and rejoining of forest and non-forest bird populations were repeated several times (see Haffer, 1967*a, d*, for further details).

The Urabá region of northwestern Colombia is of particular interest for the study of zones of apparently secondary contact of forest birds at various stages of speciation. Several of these species and semispecies pairs may have made contact here only rather recently at the end of the last severe dry phase of the Holocene. Details, however, are not yet known. (A small range gap apparently separates still today the allies of several other semispecies or species pairs of the Urabá region, such as *Columba nigrirostris* and *C. goodsoni*, *Pionopsitta haematotis* and *P. pulchra*, *Formicarius analis* and *F. nigricapillus* [Haffer, 1967*e*].) Some of the more characteristic pairs which meet in the Urabá area are given in Table 1.

In a few instances (in forms of *Pteroglossus*, *Galbula*, *Manacus*, and *Gymnostinops*) hybridization along narrow zones has been proven or seems probable (Haffer, 1967*a*). In the remaining cases the zone of secondary contact is not yet sufficiently well known to decide which one of the following situations exists: narrow overlap of two species; geographic exclusion of two ecologically competing species; or hybridization along the

TABLE 2  
COLOR CHARACTERS OF MALES OF THREE SPECIES OF *CRAX*

<i>Species</i>	<i>Legs</i>	<i>Bill</i>	<i>Cere and wattles</i>	<i>Tip of tail</i>
<i>Crax alberti</i>	flesh	greenish-gray	light blue	white
<i>Crax rubra</i>	pale gray	grayish; base, black	yellow	black
<i>Crax globulosa</i>	gray	black	yellow or red	black

zone of contact. (In two allopatric species which make contact, the peripheral populations of species A must necessarily live "within cruising range of individuals" of species B [Mayr, 1963: 672]. These peripheral *populations* of the two species might be called "sympatric." However, both *species* as such remain "allopatric" if no actual overlap of the breeding ranges is known but only a zone of contact along which the two forms meet.)

On the following pages the distribution and the presumed history of differentiation of three species pairs, of *Crax*, *Pipra*, and *Rhynchocyclus*, are discussed on the basis of my field work in the Urabá region in 1958–1959 and 1963 through 1966. The material collected has been deposited at the American Museum of Natural History, New York.

#### OBSERVATIONS ON SPECIES PAIRS

##### *Crax rubra* and *Crax alberti*

The curassows of the *Crax rubra* superspecies inhabit a vast area from Paraguay north into Mexico (Figure 2). The species ("allospecies" of Amadon, 1966) are similar in coloration and replace each other geographically, but no details of the interrelationship along the zones of contact are known for any of these forms. The Great Curassow (*C. r. rubra*) and the Blue-knobbed Curassow (*C. alberti*) meet in the Urabá region of northwestern Colombia (Figure 3). These species differ considerably in the development and pigmentation of the frontal knob and wattles in the male (Table 2) and in the plumage color of the female. They belong to different sections within the superspecies; *C. rubra* is closely related to the Amazonian *C. globulosa*, occurring well to the south, and the north Colombian *C. alberti* has its nearest ties with *C. daubentoni* to the east (Peters, 1934; Vuilleumier, 1965).

*Distribution*.—As shown in Figures 2 and 3, *Crax rubra* is a trans-Andean species and ranges continuously from western Ecuador through Central America into Mexico. In northwestern Colombia it also inhabits the hilly country east of the Gulf of Urabá where I found it at the Rio Currulao, Rio Mulatos, and Rio Naín. *Crax alberti* is known from the

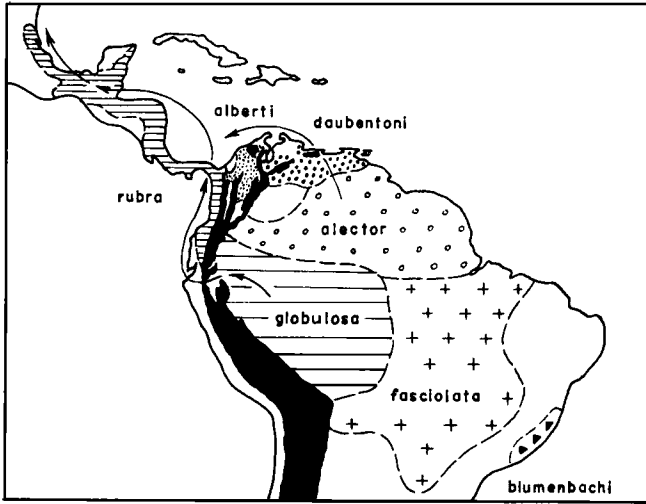


Figure 2. Distribution of the *Crax rubra* superspecies (modified from Vuilleumier, 1965: see figure 17). The Andes mountains above 1,000 m in elevation are in black. See Figure 3 for details of the zone of contact between *C. rubra* and *C. alberti*.

forested parts of the north Colombian lowlands west to the upper Sinú valley. Both species have been taken at localities only 15 and 20 km apart without any indication of interbreeding. More material should be collected before the critical populations are destroyed by the rapid deforestation, associated with agriculture, in the area of secondary contact.

*Comments.*—A similar situation is found in the species pair Salvin's Curassow (*Mitu salvini*) and Crestless Curassow (*Mitu tomentosa*). *Mitu salvini* occurs in the forests along the eastern base of the Andes of Perú, Ecuador, and Colombia north to the Macarena mountains. In the latter mountain range the species is known from Entrada camp, Cerro Macarena, and the Rio Guayabero (Blake, 1962; Olivares, 1962). *Mitu tomentosa* ranges from southern Venezuela and northern Brazil in the forests and wooded savannas westward to the eastern base of the Sierra de la Macarena. This species was collected in eastern Colombia along the Rio Apoporis (Dugand, 1952), at the lower Rio Manacacias (a tail of a subadult bird is preserved at the Instituto de Ciencias Naturales, Bogotá), near Chaffuray (de Schauensee, 1948-52), and at the Rio Guayabero (Olivares, 1962). Both species meet along the eastern and southern base of the Macarena mountains where Olivares (1962) collected specimens of *M. salvini* and *M. tomentosa* near the Guayabero river within four days of each other. This river follows the southern base of the Macarena mountains. Continuous forests cover the valleys and mountain slopes to the north and west of the "collecting locality" (campamento central, Olivares, 1962), while extensive savannas with patches of open woods and gallery forest are found in the lowlands south of campamento central on the opposite side of the Guayabero river (Olivares, 1962: figure 1). It cannot be decided today where exactly the specimens of the two species were shot, as extensive collecting trips in all directions were made by various local hunters

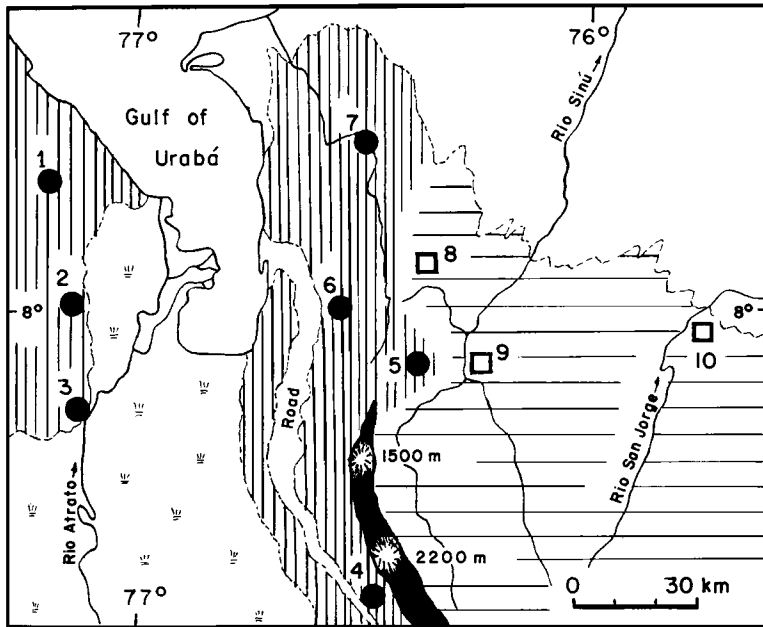


Figure 3. Distribution of *Crax rubra* and *C. alberti* in the Urabá region of north-western Colombia. Hatched vertically and circles, *Crax r. rubra*; hatched horizontally and quadrangles, *C. alberti*. Extensive swamps and lagoons are found south of the Gulf of Urabá; deforested areas are blank.

*C. r. rubra*: 1, Rio Tanela (Haffer, 1959); 2, Unguia (Blake, 1955); 3, Sautatá (de Schauensee, 1948–1952); 4, Villa Arteaga (Blake, 1955); 5, Rio Naín (Blake, 1955); 6, Rio Currulao (an immature, tame female caught in the neighboring forests; Haffer); 7, Rio Mulatos (Haffer, 1959).

*C. alberti*: 8, Quimari (de Schauensee, 1950b); 9, Socorré (read Socorro) (Blake, 1955); 10, Cativál (Blake, 1955), a village not indicated on any published map and hence not located exactly.

(Olivares, pers. comm.). *Mitu tomentosa* may have been taken in the gallery forests to the south of campamento central, while *M. salvini* probably came from the continuous forests west of the camp. Both specimens are fully adult males and do not show any indication of interbreeding. The fact that both species were taken "at the same locality" is no proof for their being sympatric breeders, as apparently implied by Vuilleumier (1965), but simply denotes the area of contact. The available evidence indicates that the species of *Mitu* replace each other geographically without interbreeding along the zones of contact. The same seems to be true also for several species of *Penelope* (Vaurie, 1966a, b).

#### *Pipra mentalis* and *Pipra erythrocephala*

These two manakins are quite different structurally as well as in coloration (Tables 3 and 4). The Red-capped Manakin (*P. mentalis*) is heavier, with a scarlet cap and yellow thighs in the male, while the smaller Flame-headed Manakin (*P. erythrocephala*) has a much shorter tail and the male has bright red and white thighs and a yellow cap. The rest of the plumage

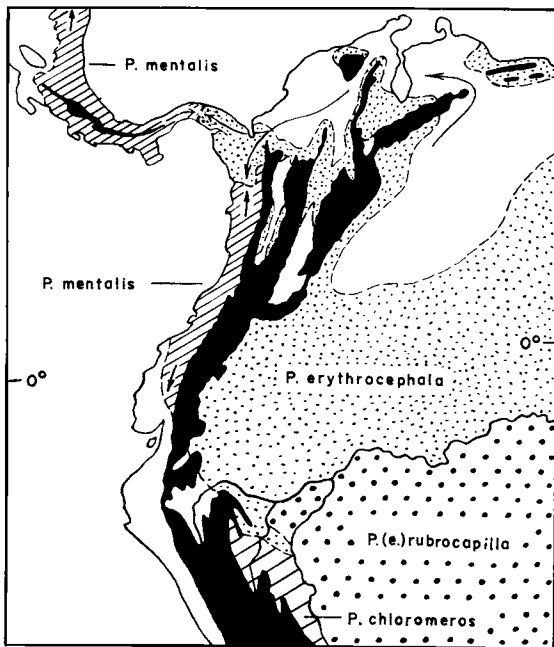


Figure 4. Distribution of the *Pipra erythrocephala* superspecies in northwestern South America and southern Central America. Elevations above 1,000 m are in black.

is of a uniform black color in both species, velvety black in *mentalis* and more blue-black in *erythrocephala*. The shafts of the secondaries are conspicuously thickened in *P. mentalis* and the tail is rather long. These structural peculiarities possibly are related to the differences noted in the courtship displays of these species—*P. mentalis* is capable of producing a loud snapping sound, with the wings (?), and a humming sound during flight, with the tail (?), which have not been heard from *P. erythrocephala* (Skutch, 1949; Snow, 1962). The latter species has normally developed secondaries and a short, stiff tail. The females and immature birds of *P. mentalis* and *P. e. erythrocephala* are very similar, but easily distinguishable on the basis of measurements.

*Distribution.*—*P. mentalis* is a trans-Andean species ranging from Mexico to northwestern Ecuador (Figures 4 and 5). A very peculiar distributional gap occurs in eastern Panamá and in the lower Atrato valley, where no specimen of this form has ever been taken. This gap is highly reminiscent of similar gaps found in other species in the same region (Haffer, 1967b).

*Pipra erythrocephala* is an Amazonian bird that apparently advanced around the northern tip of the Andes into the north Colombian lowlands.

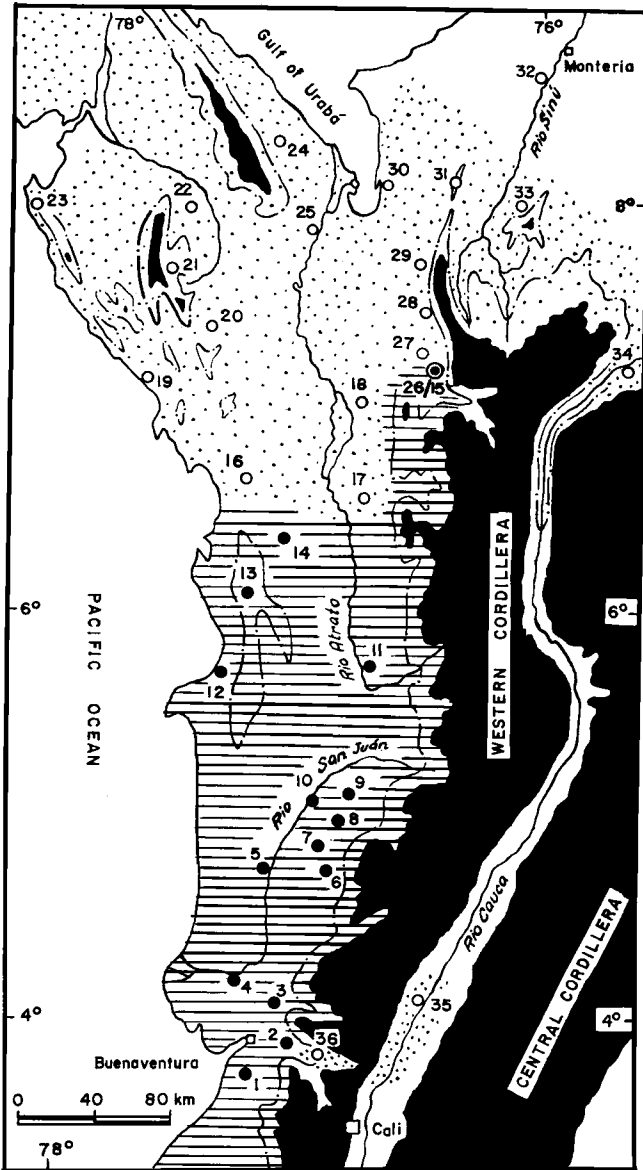


Figure 5. Distribution of *Pipra mentalis* and *P. erythrocephala* in northwestern Colombia. Hatched horizontally and full circles, *P. mentalis minor*; dotted area and open circles, *P. e. erythrocephala*. Elevations above 1,000 m in black; 500 m contour indicated by dashed and dotted line.

List of localities (if not stated otherwise, from de Schauensee, 1948-1952; specimens listed were collected by me except those from Raposo and Rio Calima):

*P. mentalis minor*: 1, Raposo (4 males and 3 females, Museo Departamental de Historia Natural, Cali); 2, San José; 3, Rio Calima (2 males and 1 female in Instituto Forestal, Medellín, coll. J. I. Borrero); 4, Malaguita; 5, Noanamá; 6, Sipí; 7, Rio Cajón; 8, Nóvita; 9, Condoto; 10, Andagoya;



TABLE 3  
CHARACTERS OF MALES OF THREE SPECIES OF *PIPRA*

Character	Species		
	<i>P. e. erythrocephala</i>	<i>P. mentalis</i>	<i>P. chloromeros</i>
Cap	yellow	red	red
Thighs	red and white	yellow	yellow
Under wing coverts	black	yellow	black
Iris	white	white	white
Tail	short	longer	broad, rounded
Shafts of secondaries	normal	thickened	thickened

It also occupies those parts of eastern Panamá and the lower Atrato valley that are not inhabited by *P. mentalis* (Figures 4 and 5).

*Comments.*—It has been claimed that both species are sympatric in eastern Panamá and northwestern Colombia (Griscom, 1929, 1935; de Schauensee, 1964). This assumption was mainly based on the record of a female of "*P. mentalis*" taken in July, 1928, from Cana, Darién (Griscom, 1929), an area otherwise inhabited exclusively by *P. erythrocephala*. This specimen is preserved at the Museum of Comparative Zoology, Cambridge (no. 140-830), and has a wing length of 56 mm and a tail of 23.5 mm (F. Vuilleumier, *in litt.*). Both measurements are too small for *P. mentalis* and are closer to *P. erythrocephala* for which species de Schauensee (1948-52: 779) gives a tail length of 18-23 mm. Mr. E. Eisenmann (*in litt.*) kindly examined this specimen and also believes it best assigned to *P. erythrocephala*. Dr. A. Wetmore (*in litt.*) collected only *P. erythrocephala* in Darién and never found the red-headed *P. mentalis*. The same is true for the adjoining area around the Gulf of Urabá where I encountered only the rather common *P. erythrocephala* (Figure 5).

Another record of *P. erythrocephala* more or less within the range of *P. mentalis* is from Cisneros (Chapman, 1917), on the western slope of the Western Andes in the Buenaventura area (no. 36 of Figure 5). This bird is preserved at the American Museum of Natural History; it is an adult male taken near Cisneros at 600 feet on 21 March 1911 by Richardson and "looks like others of its species" (E. Eisenmann, *in litt.*). There can be no doubt as to the occurrence of this species in the lower Dagua valley of the Pacific slope of the Western Cordillera. However, I do not assume a connection of the isolated Cisneros population with *P. erythrocephala* of the Urabá region. Rather, I suggest that some individuals of the Cauca valley population of *P. erythrocephala* have crossed the Western Cordillera just north of Cali to reach the Dagua valley from the east. This divide is very low and narrow in this area and was also crossed by several other forms in both directions (e.g., *Manacus vitellinus viridiventris* [Chapman, 1917]). *P. erythrocephala* most probably populated the Cauca valley near Cali by following this river valley from the north Colombian lowlands southward.

←

11, Quibdó; 12, Nuquí; 13, Baudó mountains; 14, Rio Uva (5 males); 15, Mutatá (2 males, 1 female). *P. e. erythrocephala*: 16, Rio Napipi (1 female); 17, Rio Murri (1 male); 18, Murindó; 19, Juradó; 20, Rio Salaquí; 21, Cana (Griscom, 1929; see text); 22, Rio Cupe (Griscom, 1929); 23, Mt. Sapo and Rio Jesusito (Bangs and Barbour, 1922); 24, Rio Tanela (Haffer, 1959); 25, Sautatá; 26, Mutatá (13 males, 1 female); 27, Pavarandocito (4 males); 28, Rio Imamadó (1 male); 29, Rio Chigorodó (1 female); 30, Turbo; 31, Quimari; 32, Jaraquiel (probably no longer found in this deforested region); 33, Murucú; 34, Puerto Valdivia; 35, Riofrio (not found in the Cauca valley in recent years; F. C. Lehmann, pers. comm.); 36, Cisneros.

TABLE 4  
MEASUREMENTS (IN MM) OF THREE SPECIES OF *PIPRA*<sup>1</sup>

<i>Species</i>	<i>N</i>	<i>Locality</i>	<i>Wing</i>	<i>Tail</i>	<i>Bill</i>
<i>P. e. erythrocephala</i>					
Males	6	Northwestern Colombia	54-58 (55.7)	15.5-18.5 (16.4)	7.5-8.5 (7.9)
	13	Mutatá, Antioquia	56-59.5 (57.7)	17.5-20.5 (18.3)	7.5-8.5 (8.2)
Females	8	Northwestern Colombia	56-59.5 (57.3)	17-22.5 (18.7)	8.5-9.5 (8.9)
	1	Mutatá, Antioquia	58	20	8.5
<i>P. mentalis minor</i>					
Males	4	Rio Uva, Chocó	59.5-62 (60.7)	26-27.5 (26.8)	8.6-9.4 (9.1)
	2	Mutatá, Antioquia	61; 62	27; 26	9; 9
Females	3	Chocó region	60-62.5	26-29 <sup>2</sup>	9-10.5
	1	Mutatá, Antioquia	62	29.5	9
<i>P. chloromeros</i>					
Males	2	Bala, Beni, Bolivia (Mus. Koenig, Bonn, Germany)	60.5; 63 63.5	26.5; 26.5	—; 9

<sup>1</sup> Ranges; means (in parentheses) are given for samples of four or more.

<sup>2</sup> From de Schauensee (1948-1952: 779).

*Species limits.*—*P. mentalis* and *P. erythrocephala* are strictly allopatric, no overlap of their ranges being known so far. In eastern Panamá *P. mentalis* is found east to the Rio Chepo area where it meets the westwardly advancing *P. erythrocephala*. The latter species was also taken at the Rio Chepo (Griscom, 1933). This of course does not prove sympatric breeding of the two species which simply made contact in this area. On the Caribbean coast the zone of contact of these two species may be located at the Golfo de San Blas to the north of the Chepo region.

In the Atrato valley of northwestern Colombia I traced *P. erythrocephala* south to the Rio Murri and the Rio Napipi and found *P. mentalis* 30 km to the south at the Rio Uva (Figure 5). East of the Atrato river both species meet near Mutatá (nos. 26 and 15 of Figure 5) where I collected them within only 100 meters of each other.

*Comments.*—Continuous forests cover the mountains of the Western Andes to the east of Mutatá and the hilly country to the west of this village. Large clearings have appeared only along the road from Dabeiba to Turbo. Mutatá is located where this road is crossed by the Rio Mutatá, which flows into the nearby Rio Sucio. A narrow gravel road is being constructed in untouched rain forest from Mutatá to Pavaran-docito and Murindó in the Atrato valley. This road crosses the Rio Sucio near Mutatá and was traversable for about five kilometers to the southwest of Mutatá during the

time of my visit in August, 1966 (Haffer, 1967e: figure 5-7). I have not found either species on the steep mountain slopes to the east of Mutatá but only in the forests covering the level river terraces of the Rio Sucio and the hilly country farther southwest. At kilometer 3 and just north of the above-mentioned gravel road I encountered several groups of adult males of *P. erythrocephala* and collected 11 males and one female. At kilometer 4.5, west of the Oquendo creek, and southwest of the road which here turns to the northwest, one male and one female of *P. mentalis* were obtained and another male observed. In this same area and only about 100 meters from the spot where *P. mentalis* was taken one male of *P. erythrocephala* was collected. A second male of *P. mentalis* was taken while it was foraging about 700 meters south of kilometer 2.5 of the gravel road. On this same forest trail and closer to the road a lone foraging male of *P. erythrocephala* was observed.

The series of *P. erythrocephala* from Mutatá (12 ♂♂ and 1 ♀) is perfectly typical, although in average size it is at the upper limit of the range observed in northwestern Colombia (Table 4). Some variation in the yellow color of the head in males is visible in the above series, but this is also characteristic for other populations within the wide geographical range of this species (Hellmayr, 1929). In most of the males from Mutatá the coloration of the head agrees with that of specimens from the Urabá region to the north and from the humid middle Magdalena valley. Three males are distinguished by a slightly deeper orange-yellow hue. This difference, however, is considered to be within the limits of individual variation and should not be interpreted as evidence for introgression of *mentalis* genes. The female, although also entirely typical, is somewhat more richly colored above and below than specimens from the (less humid) lowlands around the Gulf of Urabá to the north.

The three specimens of *P. mentalis minor* (2 ♂♂ and 1 ♀) collected southwest of Mutatá are also typical for this form and agree in size and coloration with birds from the Chocó region to the south (Table 4).

It is obvious from the above data that *P. mentalis* and *P. erythrocephala* meet southwest of Mutatá without interbreeding. *P. mentalis* is much rarer than *P. erythrocephala*; the above-mentioned four individuals (three specimens and one sight record) were the only ones seen during 13 days of collecting in the forests. Nothing was noted in the material collected which might be interpreted as evidence of introgression of genes of the respective ally. I conclude that the two species compete ecologically and for this reason replace each other geographically. The range limit of both species probably is not a straight line but rather irregular in detail as shown by a single male of *P. erythrocephala* collected near the Rio Piedras Blancas and not far from the main road, 10 km south of Mutatá. *P. mentalis* probably still inhabits the forests covering the hills and mountains to the south and southwest of Mutatá, while *P. erythrocephala* ranges north and northwest of this village. Changes of the location of the zone of contact may be brought about by the human disturbances of the forests. Thus a future visitor to this region might find a situation different from that which I encountered in 1966. The forests along the gravel road from Mutatá to Pavarandocito and Murindó will soon be cut by settlers who already have acquired the property rights of these areas.

*Ecology.*—In western Colombia *P. mentalis minor* inhabits the extremely humid forests (Wet and Pluvial Forest) and is replaced by *P. erythrocephala* in areas where the annual precipitation is considerably lower, with a marked dry season being developed, from Rio Napipí and Mutatá to the north (Moist and Dry Forest). On the other hand Eisenmann (*in litt.*) has found *P. mentalis ignifera* of central Panamá not only in the more humid areas, but also in open woodland and shady second growth of fairly humid areas and even in woodland within the municipal limits of Panamá City. This indicates that this species probably would occupy large parts of Darién and the Urabá region were it not for the presence of *P. erythrocephala* in these areas. The same is true for *P. e. erythrocephala*, which form would presumably advance farther into central Panamá but for the presence of *P. mentalis ignifera*.

I have met both species in Colombia in the forest interior, mostly along low ridges where the visibility was slightly better than in the dense, tangled vegetation near creeks in the neighboring valleys.

*Amazonian relatives.*—*P. mentalis* is very close in size and coloration to *P. chloromeros* (see Tables 3 and 4) which inhabits the eastern foothills of the Peruvian and Bolivian Andes (Figure 4). They differ in the color of the under wing coverts of the male which are yellow in *P. mentalis* and black in *P. chloromeros* and strikingly in shape of the tail, which is rounded and broad in *P. chloromeros* and square-tipped or slightly emarginate and narrow in *P. mentalis*. *P. chloromeros* meets *P. erythrocephala* and *P. (e.) rubrocapilla* in the upper Amazonian lowlands. The available locality records (Hellmayr, 1929; de Schauensee, 1953) seem to indicate that these species are also allopatric (Figure 4). *P. erythrocephala* and *P. (e.) rubrocapilla* apparently meet at Sarayacu, near which locality both forms have been collected (de Schauensee, 1966). Possibly, then, *P. erythrocephala* and *P. chloromeros* + *mentalis* can be considered as members ("allospecies"; Amadon, 1966) of a superspecies.

#### *Rhynchocyclus brevirostris* and *Rhynchocyclus olivaceus*

The Eye-ringed Flatbill (*R. brevirostris*) and Olivaceous Flatbill (*R. olivaceus*) are rather inconspicuous, medium-sized flycatchers that inhabit forest and forest borders. Both are very similar in size and coloration and are distinguished in the field only with difficulty. *R. brevirostris* is dark olive green above and on the breast, and its dusky remiges have margins of olive green to tawny olive; *R. olivaceus* is lighter olive green and shows yellowish olive margins to the remiges. The bill is somewhat broader and heavier in *R. brevirostris*.

*Distribution.*—*R. brevirostris* occurs west of the Andes from Mexico south to northwestern Ecuador. The species is not known from the low-

lands of central and eastern Panamá and the lower Atrato valley of northwestern Colombia. However, it inhabits the higher levels of the mountains of southeastern Darién. *R. olivaceus* is mainly distributed in the Amazonian lowlands and apparently advanced around the northern tip of the Andes into northern Colombia. It occupies the lowlands of eastern and central Panamá and the lower Atrato valley which are not inhabited by *R. brevirostris*.

*Comments.*—In Middle America *R. b. brevirostris* and *R. b. pallidus* inhabit suitable forests or adjacent second growth from sea level to the subtropical or even the temperate zone (Skutch, 1960; Slud, 1964; Binford, 1965). E. Eisenmann (*in litt.*) states that:

. . . *brevirostris* of western Panamá is essentially montane, occurring chiefly between 3,000–7,000 feet, although I know of records from 1,200–2,500 feet, farther east in Veraguas and in Herrera provinces (Azucero peninsula), where the mountains are lower than in Chiriquí. However, I know a few Chiriquí specimens from the tropical zone at Bugaba and Divala (possibly birds that descended during the dry season?).

Aldrich (1937) also reported *R. brevirostris* from the Azucero peninsula at only 250 feet elevation in the tropical zone, which might indicate that this species in western Panamá, although mainly inhabiting the forested slopes of the mountains, does not avoid the lowlands completely.

In eastern Panamá (Darién) *R. brevirostris hellmayri* is strictly confined to the higher levels of isolated mountain peaks, such as Mt. Pirrí and Mt. Tacarcuna, where it was taken at 4,600 feet.

In western Colombia, *R. b. pacificus* inhabits the humid lowlands of the Chocó region from Mutatá and the Rio Uva to the south (Figure 6) and was taken at 3,000 feet on the Alto del Buey and at 2,500 feet near Santa Cecilia on the western slope of the Western Andes. An isolated record from the Rio Truandó in the lower Atrato valley (Cassin, 1860) falls into the range of *R. olivaceus*; it would not be impossible to find a straggler of the Pirrí population of *R. b. hellmayri* in the Truandó area since a bird could have followed the "Serranía de los Saltos" southward. Unfortunately the bird on which the record rests cannot be found in the collections of the Philadelphia Academy of Sciences and was probably discarded long ago (R. M. de Schauensee, *in litt.*). For this reason the remote possibility of a misidentification cannot entirely be ruled out (see Hafler, 1967*b* for other problematic records from the Truandó region).

The lighter-colored Olivaceous Flatbill reaches its western range limit in central Panamá. In this area it inhabits the lowlands that are left unoccupied by *R. brevirostris*. The only locality from which both species have been reported is Cana, Darién, in eastern Panamá (Griscom, 1929, 1932), and it is probable that the collecting sites were at different elevations. In the lower Atrato valley, *R. olivaceus* advances south to the Rio Sucio (Pavandocito) and the Rio Napipi.

*Species limits.*—We find that both species replace each other geographically in the lowlands of northwestern Colombia and central Panamá. In eastern Panamá they occur in the same general area but cannot be considered sympatric breeders as they inhabit different altitudinal life zones. It is of considerable interest to find out the interrelationship of both forms in the zones of contact. For this reason I have made a special effort dur-

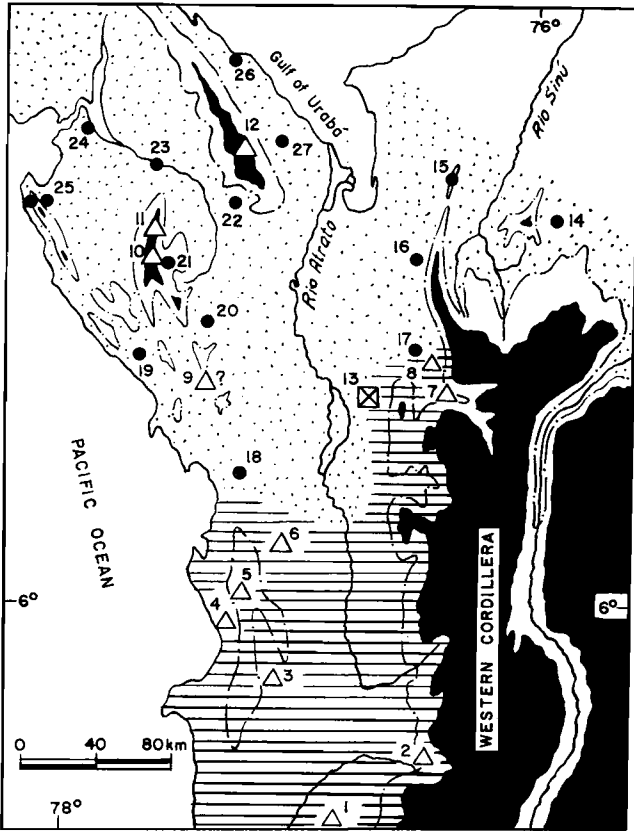


Figure 6. Distribution of *Rhynchoicyclus breviostris* and *R. olivaceus* in northwestern Colombia and southeastern Panamá. Hatched horizontally and open triangles, *R. breviostris*; dotted area and full circles, *R. olivaceus*; crossed quadrangle, *R. "olivaceus mirus."* Elevations above 1,000 m are in black; the 500 m contour line is indicated with a dashed and dotted line.

List of localities (if not stated otherwise, from de Schauensee, 1948–1952; specimens listed were collected by me):

*R. breviostris pacificus*: 1, Növita and Juntas de Tamaná; 2, Santa Cecilia; 3, Rio Baudó; 4, Rio Jurubidá; 5, Alto del Buey; 6, Rio Uva (2 males, 1 female); 7, Alto Bonito; 8, Mutatá (2 males, 1 female).

*R. breviostris hellmayri*: 9, Rio Truandó (see text for discussion of this doubtful record); 10, "Cana" (Griscom, 1932); 11, Mt. Pirri (Griscom, 1935); 12, Mt. Tacarcuna (Griscom, 1932).

*R. "olivaceus mirus"*: 13, Murindó.

*R. olivaceus bardus*: 14, Sitio Nuevo, upper Rio San Jorge (1 male); 15, Quimari; 16, Rio Chigorodó (1 female); 17, Pavarandocito (1 male); 18, Rio Napipí (1 male); 19, Rio Juradó; 20, Rio Salaquí (1 male, 1 female); 21, Cana (Griscom, 1929, 1932); 22, Tapalisa (Zimmer, 1939); 23, El Real (Zimmer, 1939); 24, Chepigana (Zimmer, 1939); 25, Rio Jesusito and Mt. Sapo (Bangs and Barbour, 1922); 26, Puerto Obaldia, Permé, and Ranchón (Griscom, 1932); 27, Rio Tanela (Haffer, 1959 [erroneously listed as *R. breviostris*]).

ing my recent field work to obtain material from the lower Atrato valley. The specimens I collected in this area, south to Pavarandocito and the Rio Napipí (Figure 6), agree with *R. olivaceus bardus* of northwestern

Colombia and eastern Panamá, and I took a small series of *R. brevirostris pacificus* in the Rio Uva valley and at Mutatá. No evidence of introgression is seen in any of these birds. The three specimens obtained at kilometers 4.5 and 2.5 of the new gravel road southwest of Mutatá (see p. 353) are clearly referable to *R. brevirostris pacificus* on the basis of their heavy bills and rich plumage coloration. The pair taken at km 4.5 is slightly paler below than the male taken at km 2.5. However, the latter bird is freshly molted, while the other two specimens are in old plumage. The observed differences are probably due to wear. It should be noted that the Mutatá locality is only about 10 km from Pavarandocito, where I have collected a bird in the typical plumage of *R. olivaceus bardus*.

In the Urabá region I found no specimens of *R. olivaceus mirus*, a subspecies described by de Schauensee (1950a) from Murindó on the lower Atrato river. After comparing the color characters and the geographical distribution of the various *Rhynchocyclus* forms I now feel that "*R. olivaceus mirus*" may turn out to represent a hybrid population of *R. olivaceus bardus* and *R. brevirostris pacificus*. The intermediate color characters (in body color "*mirus*" is like *R. olivaceus bardus*, but the edges of the wing feathers are colored as in *R. brevirostris pacificus*), the geographical occurrence in the expected zone of contact of both species (Figure 6), and the very restricted range would favor this interpretation.

Mr. de Schauensee has kindly compared the original specimens of "*mirus*" with both *R. olivaceus* and *R. brevirostris* and writes me: "you may well be right in your impression that the bird is a hybrid. We have four specimens of it all exactly alike." It should be pointed out, however, that the latter statement referring to the non-variable coloration of these four individuals would not support the view that these birds were taken from a hybrid population. Certainly more material is needed from the critical area of geographic replacement to determine the situation. Data from central and western Panamá, where both species also meet in Coclé province would be of particular interest. Skutch (1960) has studied *R. brevirostris* and *R. olivaceus* in life without noting any differences in behavior, calls, and nests. He therefore "wonders what prevents their interbreeding if they do actually come in contact" (1960: 514).

#### DISCUSSION

In contrast to various published accounts, the members of the species pairs which I have studied are strictly allopatric in the lowlands of north-western Colombia. They probably have different ecologic preferences, each form being better adapted to different ranges or sets of ecologic influences, such as temperature, humidity, vegetation, etc. However, for most of these species there are no indications that they reach their limit

of tolerance for environmental conditions at the zone of contact. It seems very probable that the species of *Crax* as well as *Pipra erythrocephala*, *P. mentalis ignifera*, and *Rhynchocyclus olivaceus bardus* would occupy at least parts of the ranges of their allies were it not for the presence of the latter across the zone of contact. The northern range limits of *Pipra mentalis minor* and *Rhynchocyclus brevirostris pacificus* in the lower Atrato valley may, however, also correspond to the ecologic limit of these two forms which are adapted to the extremely humid climatic conditions of the Chocó lowlands. These subspecies do not occur north of Mutatá and the Baudó mountains, where the annual rainfall decreases considerably.<sup>1</sup> Although this conspicuous climatic gradient is responsible for important faunal differences between the Urabá and Chocó regions, it is certainly not steep enough to account for the abrupt geographic replacement of the members of species pairs. Probably a balanced situation has been reached today with each form at a competitive advantage over its ally in the area occupied. This raises the problem of a possible shift of the location of the zones of contact since the time the allies met in northwestern Colombia. For example, it could be argued that the presumably more successful Amazonian *Pipra erythrocephala* actively separated the previously continuous range of *Pipra mentalis*, forcing the latter species out of the Urabá and eastern Darién regions. Similarly, it could be assumed that the presently isolated populations of the trans-Andean *Rhynchocyclus brevirostris* have been continuous before the arrival of the cis-Andean (i.e., east of the Andes) *R. olivaceus* which species presumably forced *R. brevirostris* to retreat into Central America, south into the Chocó region, and up onto the higher mountains of eastern Darién. However, I favor another explanation based on the characteristics of the Pleistocene and post-Pleistocene climatic history of tropical South and Central America (Haffer, 1967a). The distributional gaps in the range of the trans-Andean forms probably originated during dry climatic periods when the Urabá and Darién regions were covered with drier types of vegetation, too dry for many forest birds. The cis-Andean allies subsequently occupied these areas upon the return of heavier forest growth and more humid climatic conditions before the trans-Andean forms could do so. An adjustment of the location of the zones of contact, possibly involving a shift of several kilometers, may have taken place at the time the allies made contact but, I think it was regionally of minor importance.

The above historical interpretation is supported by the following facts. A somewhat similar distributional gap in northwestern Colombia or in

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<sup>1</sup> The fact that many Chocó forms occur considerably farther north along the base of the Western Andes than along the Pacific coast on the opposite side of the Atrato valley (Figures 5 and 6) may be explained ecologically (Haffer, 1967e).



parts of Panamá, or in both, is also found for several trans-Andean species pairs whose Amazonian representatives did not advance into northwestern Colombia. Examples are *Carpodectes nitidus* and *C. hopkei*, *Cotinga amabilis* and *C. nattererii*, *Gymnostinops montezuma* and *G. guatimozinus*. E. Eisenmann (*in litt.*) pointed out that in all these cases there seems to be a gap where neither ally occurs, while in the cases of *Pipra* and *Rhynchocyclus* one or the other seems to be present in all suitable habitats. Despite this difference the explanation of the distributional gaps between the allies of *Carpodectes*, *Cotinga*, and *Gymnostinops* on the basis of the Pleistocene climatic cycles seems to me to be very reasonable too. This is indicated by an interesting intermediate situation shown by the present distribution of the forms of *Galbula ruficauda*. The gap between the Central American and the west Colombian population of *G. (r.) melanogenia* comprises central and eastern Panamá and the lowlands around the Gulf of Urabá. This gap was only partially filled by the cis-Andean *G. ruficauda* which form occupied only the Urabá region without advancing westward into Panamá (Haffer, 1967a).<sup>2</sup> The separation of the Central American and west Colombian populations of *G. (r.) melanogenia* is here obviously not related to the invasion of *G. ruficauda* from the east. I assume the latter cis-Andean form encountered unoccupied terrain in the Urabá region at the time of arrival but did not take full advantage of the given opportunities, leaving eastern and central Panamá uninhabited (an area probably ecologically suited to this bird today). In this case the Central American population of *G. (r.) melanogenia* did not reoccupy central and eastern Panamá for unknown reasons.

The two species of *Crax* discussed in this article are separated by the high range of the "Serranía de Abibe" which reaches elevations of 2,200 and 1,500 meters southeast of the Gulf of Urabá (Figure 3). Both forms meet today along the northern extension of this mountain range where its elevation gradually decreases and thus permits the contact of the eastern *C. alberti* and the western *C. rubra*. There is no indication of any appreciable shift of the zone of contact in this case either.

On the basis of the foregoing discussion I conclude that the geographic replacement known in various species pairs of Panamá or northwestern Colombia, or in both, still occurs today in the area where the allies met in the recent geologic past.

Speciation seems not to be fully completed in the allies of *Crax*, *Pipra*, and *Rhynchocyclus* treated in this article. Indications for local interbreeding, however, are only known so far in the *Rhynchocyclus* forms and

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<sup>2</sup> Two fledgling specimens of *G. r. ruficauda* taken by Mr. Peter Slattery at the Rio Pirri, 3 mi. S. of El Real, in April, 1966 (E. Eisenmann, *in litt.*), show that this bird actually did enter easternmost Panamá in the Tuira valley.

the evidence even of this is slight. Hybrids between *Crax rubra* and *C. alberti* have been obtained in captivity (Taibel, 1950). Possibly under natural conditions, premating sexual isolating mechanisms (Mayr, 1963: 92-104), such as differences in the courtship displays of the males, etc., are active in the species of *Crax* and *Pipra*, and actual interbreeding is prevented. A similar situation may also exist in the species of *Mitu* and *Penelope* mentioned above (page 348). The allies probably became reproductively isolated during geographic separation but remained sufficiently competitive to hold each other off. Such strict geographic replacement as a result of ecologic competition is known among birds in only a few well studied cases. Stresemann (1939: 361) lists examples from the Old World and Selander and Giller (1963: 257) and Brewer (1963) reported several cases in New World woodpeckers and tits, respectively. The range of some west Ecuadorian wrens (Selander, 1964), trogons and tanagers (Haffer, 1967*d*), and of west Peruvian species of *Geositta* (Koepcke, 1965: 157) may also be limited by interspecific competition.

The members of the species pairs of northwestern Colombia came into contact possibly only several thousand years ago when, after a sub-Recent period of drought, the forests were united in the Urabá region. However, we do not know for how long the forms had been isolated before. I assume that the trans-Andean populations did not occupy the lowlands west of the Andes before the final connection with the Amazonian lowlands was established at the end of Tertiary time. The differentiation of the trans-Andean species is thus related to the Pleistocene climatic history rather than to the Tertiary orogenic development of the northern Andes (Haffer, 1967*a*). This is in accord with the findings of Vuilleumier (1965) who concluded that within various genera of cracids speciation is in early stages and probably occurred as late as the Pleistocene. Supporting evidence for the occurrence of comparatively recent (Pleistocene) speciation in many bird families has been discussed by Moreau (1966*a*, *b*: 9-12).

The discussion of the presumed history of the trans-Andean species *Crax rubra* and *Pipra mentalis* suggests that present distribution cannot be considered a very useful criterion in these cases to establish the geographic origin of the species. Range extensions after differentiation may have been so considerable as to render extremely speculative any conclusion drawn from present distribution alone. Both *Crax rubra* and *Pipra mentalis* have a most extensive range in Central America north to Mexico, and the latter species even has two subspecies in this area. This might lead one to assume that these species originated in Central America. However, on the basis of their close relationship to forms inhabiting the eastern foothills of the Peruvian Andes, I strongly suspect that their ancestors

reached the Pacific lowlands from upper Amazonia by crossing the north Peruvian Andes, which may have been somewhat lower at that time. In my view, *Crax rubra* and *Pipra mentalis* advanced into Central America after they had been differentiated in the Chocó Refuge of western Colombia.

On the other hand, the ancestor of *Crax alberti* probably advanced into northern Colombia from the east and was possibly later isolated in the Nechí Refuge at the northern foot of the Western and Central Andes. Thus we have the interesting case of two forms, *C. rubra* and *C. alberti*, whose ancestors in the first case probably crossed the Andes, possibly in northern Perú, and, in the second instance, probably came around the northern tip of the mountain ranges from the east. The conspicuous morphological gap between *C. rubra* and *C. alberti* and the close relationship of these forms with *C. globulosa* and *C. daubentoni*, respectively, seems best explained by a northward-directed dispersal pattern of the *Crax rubra* superspecies as illustrated in Figure 2. The explanation of the above situation at the entrance into South America would meet considerable difficulties if the opposite assumption were made—that is, a dispersal of this superspecies from Central into South America. In my view, the ancestor of the *C. rubra* superspecies had developed in tropical South America by the end of the Tertiary and dispersed widely during the Pleistocene, entering Central America from the south. Future investigations may alter this interpretation which, admittedly, is based on rather scanty and indirect evidence.

Recently Vuilleumier (1965) postulated that the 9 or 10 ancestors of the present South American cracids arrived in South America from the north as recently as the early Pleistocene. Such a late "passing through Central America" of a comparatively large number of birds, which is not reflected in present distribution, seems very unlikely. I would expect to find in Central America today at least some descendents of these northern immigrants (which could have survived in the various forest refugia) if a wave of early Pleistocene cracids had passed from North into South America. But there are none. The only cracids presently found in Central America are young, probably Pleistocene, arrivals from the south (*Crax*, *Chamaepetes*, *Penelope*, *Ortalis*) and forms which may or may not have originated in this area from South American ancestors presumably during the Upper Tertiary (*Oreophasis*, *Penelopina*). The present South American cracids possibly originated from a number of ancestors which radiated in South America during the Tertiary. It is not known whether this radiation was secondary (Mayr, 1964) or primary. The fossil cracids known from North America and the favorable ecologic conditions in this region during the

Tertiary (Vuilleumier, 1965) do not disprove the possibility that cracid immigrants from South America have reached Central and North America repeatedly during early and mid-Tertiary time. The North American members of the family became extinct when the climate deteriorated at the end of the Tertiary. On the other hand, the Pleistocene climatic changes of tropical South America caused repeated isolation and permitted frequent rejoining of cracid populations through the changing distributions of forest and non-forest vegetation. In this way it favored the development of widely distributed "genera" composed of allopatric and often only weakly differentiated species.

The populations of *Rhynchocyclus brevirostris* which were isolated in the Chocó Refuge of western Colombia and in the Central American Refugia represent today *R. b. pacificus* and *R. b. brevirostris* + *pallidus*, respectively. The occurrence of *R. b. hellmayri* in eastern Panamá indicates a former connection of the Central American and west Colombian populations. *R. b. hellmayri* probably was differentiated in isolated forests which remained on the mountain slopes of southeastern Darién (Mt. Pirrí, Mt. Tacarcuna) during dry climatic phases of the Pleistocene. Upon the return of more humid conditions, the Amazonian *Rhynchocyclus olivaceus*, coming around the Andes in the north, advanced into the lower Atrato valley and Panamá and occupied the lowlands which had been left uninhabited by *R. brevirostris* because of ecological reasons.

It remains questionable whether *R. brevirostris* originated in the Chocó Refuge and then moved northward, or whether it was differentiated in Central America, and subsequently extended its range southward into the Chocó region. The case of the *Rhynchocyclus* species is of particular interest, since both forms replace each other geographically, and possibly hybridize locally where they meet in the lowlands of the lower Atrato valley. In eastern Panamá, however, they occur in the same general region, inhabiting different altitudinal zones. For this reason they are best treated nomenclaturally as "good species."

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## SUMMARY

Contrary to published accounts, the members of the following species pairs replace each other geographically where they meet in the forested lowlands of northwestern Colombia: *Crax r. rubra* and *C. alberti*; *Pipra mentalis minor* and *P. e. erythrocephala*; and *Rhynchocyclus brevirostris pacificus* and *R. olivaceus bardus*.

Hybridization between the forms of *Rhynchocyclus* may occur locally. However, no evidence of interbreeding is so far known in the members of the other two species pairs, which differ considerably in structure and coloration. It is assumed that they replace each other geographically as a result of ecologic competition.

The species treated here are members of superspecies with wide ranges in Central and South America. The present ranges and morphologic relations of these various species suggest a northward-directed dispersal pattern of the superspecies, from the Amazonian lowlands as a center, into the Pacific lowlands west of the Colombian Andes and north into Central America. The differentiation of the species probably was closely related to Pleistocene climatic history rather than to the Tertiary paleogeographic and orogenic development of the Neotropical Region.

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