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SPECIATION IN THE CARBONATED FLOWER-PIERCER (*DIGLOSSA CARBONARIA*) COMPLEX OF THE ANDES

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ABSTRACT.—The evolution, differentiation, and present distribution of the Carbonated Flower-Piercer (*Diglossa carbonaria*) superspecies were apparently greatly affected by Pleistocene glacial cycles. Populations of the six principal morphotypes are now largely allopatric, although secondary contact occurs in northern Peru (*aterrima* and *brunneiventris*) and northwest Bolivia (*brunneiventris* and *carbonaria*). A narrow zone of hybridization between *brunneiventris* and *carbonaria* occurs northeast of La Paz, Bolivia. The presence of hybrid-like individuals in allopatric populations from eastern Bolivia (*carbonaria*), Colombia (*humeralis*), and Venezuela (*gloriosa*) may be due to past genetic contact and not to present introgression from nearby forms. The forms *aterrima*, *humeralis*, and *nocticolor* are closely related and conspecific (*D. humeralis*). The form *gloriosa* is a distinct allospecies (*D. gloriosa*). The Colombian population of *brunneiventris* is subspecifically distinct from the nominate form. The forms *brunneiventris* and *carbonaria* are closely related, but assuming the existence of a partial isolating mechanism between them, should be recognized as allospecies (*D. brunneiventris* and *D. carbonaria*). I present a model of speciation that accounts for the disjunction of similar phenotypes. I propose that differentiation in isolation occurred in a number of high Andean forest refuges during Pleistocene glacials and interglacials, and that dispersal and genetic contact occurred with altitudinal changes in timberline forest at the beginnings and terminations of glacial periods.

The Andes Mountains of western South America are among the most biotically complex but least studied highland tropical regions in the world. Several workers have examined the effects of Pleistocene climatic shifts on the differentiation of part of the Andean biota (e.g., Haffer 1967, 1969, 1974; F. Vuilleumier 1969a, 1970a, 1981a; B. Vuilleumier 1971; Van der Hammen et al. 1973; Van der Hammen 1974; Simpson 1975; Simpson and Haffer 1978; Vuilleumier and Simberloff 1980). However, until recently, the paucity of distributional and life history information prevented detailed analysis of avian speciation in the Andes. In the tradition of Chapman's (1917, 1926) pioneering works on Andean birds, F. Vuilleumier (1968, 1969b, 1970b, 1971), Paynter (1972, 1978), Fitzpatrick (1973), and Carpenter (1976) have now detailed specific patterns of speciation in several groups of subtropical and temperate to paramo-puna zone birds.

The flower-piercers (*Diglossa*) consist of several groups of species restricted to the highland forest and shrubland of the neotropics from Mexico south through Central America

to northern Argentina. These primarily nectarivorous and insectivorous nine-primaried oscines reach their greatest diversity in the Andes (Colombia south to Bolivia), where up to seven species occur on an altitudinal gradient. The high Andean *Diglossa carbonaria* superspecies inhabits "ceja" and timberline shrubland (1,500 to 4,000 m) from the Sierra Nevada de Santa Marta in northern Colombia south through Ecuador and Peru to northern Chile and Bolivia (Fig. 1). This polytypic group (Table 1) has previously attracted the attention of researchers (Zimmer 1929, Vuilleumier 1969b, unpubl. observ.) because it provides an outstanding example of speciation in progress.

One of the most perplexing problems confronted by a systematist is divining the taxonomic status of allopatric taxa (Mayr 1963). The *D. carbonaria* superspecies is composed of a confusing variety of largely allopatric groups at and below the specific level that at first glance seem to be distributed in a chaotic manner (Fig. 1). Since the 1838 description of the Carbonated Flower-Piercer (*D. carbonaria*, Lafresnaye and d'Orbigny), the systematic relationships of named taxa of *Diglossa*

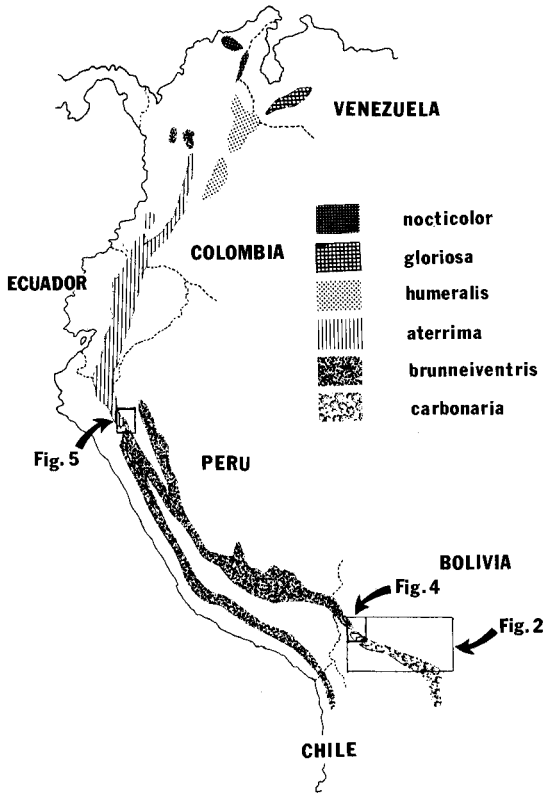


FIGURE 1. Present distribution (highly schematic) of the *D. carbonaria* superspecies in the Andes Mountains of western South America (redrawn from Vuilleumier 1969b). The distribution of *brunneiventris* on the western slope of the Andes between central Peru and northern Chile is based on LSUMZ specimens and personal observations. Colombian *brunneiventris* are subspecifically distinct from the nominate form found in Peru and Bolivia (Graves 1980).

have been uncertain. On the basis of morphological similarities and coincidental distribution, Stresemann (in Zimmer 1929) grouped certain members of the genus into "Formenkreise." The forms *gloriosa* and *humeralis* of the *D. carbonaria* superspecies were grouped, respectively, with *gloriosissima* and *lafresnayii* of the *D. lafresnayii* superspecies (Glossy Flower-Piercer).

Zimmer (1929) was the first to recognize the superspecific relationship of the six forms of the *carbonaria* group, which he considered as conspecific on the basis of group characteristics. The subsequent classification by Hellmayr (1935) followed Zimmer in treating *D. carbonaria* as a polytypic species. However, in a recent monograph concerning the genus *Diglossa*, Vuilleumier (1969b) provided additional information about the development of isolating mechanisms and secondary contact in *D. carbonaria*. He considered it a superspecies with two semispecies, nomenclaturally treated as species: *D. humeralis* (*humeralis*, *aterrima*, *nocticolor*) and *D. carbonaria* (*carbonaria*, *brunneiventris* and *gloriosa*). In a recent reappraisal of the group, Vuilleumier (unpubl. observ.) considered *gloriosa* an allospecies (along with *D. humeralis* and *D. carbonaria*).

Past systematic studies have dealt primarily with documenting morphological differentiation and location of barriers to gene flow. In this study of the *D. carbonaria* superspecies, I attempt to determine population structure of taxa and to correlate speciation with presumed Pleistocene climatic events.

METHODS

My investigations of phenotypic variation in the *D. carbonaria* superspecies involved the detailed examination of 1,010 museum specimens (134 *carbonaria*, 358 *brunneiventris*, 279 *aterrima*, 80 *humeralis*, 127 *nocticolor*, and 32 *gloriosa*) together with field studies in the Peruvian Andes.

I conducted field investigations during 1976–1978 in the Department of Cajamarca, northern Peru, as follows (actual field days): 2–5 September 1976 and 1 September 1977 at Colmena, 20 km NE Llama, 2,675 m; 2–5 September 1977 and 8–22 June 1978, near Cutervo, 2,600 m; 6–12 September 1977, NE of Chota, 2,670 m; and 13–19 September 1977, along a transect between Lajas and Cutervo, 2,600 to 3,000 m.

TABLE 1. Color patterns of taxa in the *D. carbonaria* superspecies.

	<i>aterrima</i>	<i>nocticolor</i>	<i>humeralis</i>	<i>carbonaria</i>	<i>gloriosa</i>	<i>brunneiventris</i> *
Base of lower mandible	Black	Bluish gray	Bluish gray	Bluish gray	Bluish gray	Bluish gray
Rump	Black	Gray	Gray	Gray	Gray	Gray
Shoulders	Black	Black	Gray	Gray	Gray	Gray
Crissum	Black	Black	Black	Rufous	Rufous	Rufous
Lower breast and belly	Black	Black	Black	Gray	Rufous	Rufous
Superciliary line	Absent	Absent	Absent	Absent	Present	Present
Malar mark	Absent	Absent	Absent	Absent	Absent	Present

* Colombian populations (*vuilleumieri*) average smaller in wing, tail, and tarsus measurements than Peruvian specimens.

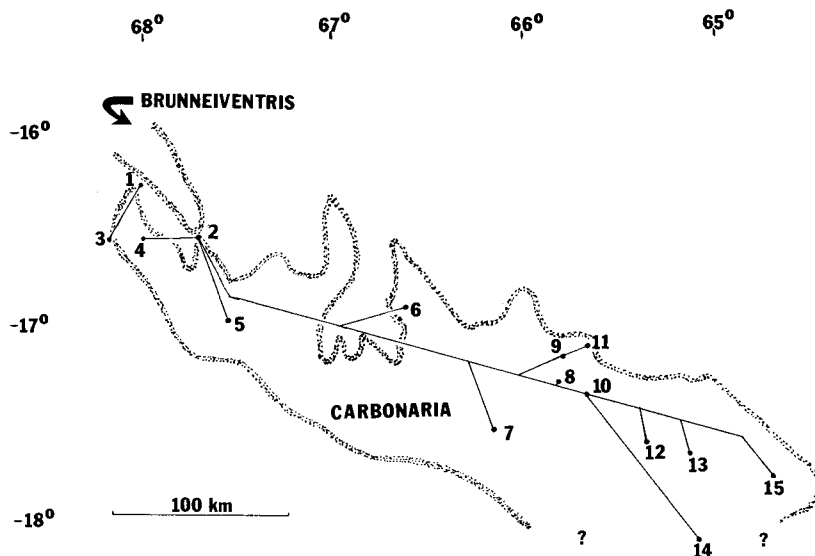


FIGURE 2. Collection sites in Bolivia: (1) Caxata, (2) Iquico, (3) Palca, (4) Calacoto, (5) Tanapaca, (6) Chorros, (7) Parotani, (8) Colomi, (9) Incachaca, (10) Tiraque, (11) Chapare, (12) Pocona, (13) Titora, (14) Aiquile, (15) Comarapa. For location of the area shown here, see Figure 1. Stippled lines surround the approximate ranges of *carbonaria* and *brunneiventris*. Distances between sites where *carbonaria* was collected and the nearest populations of *brunneiventris* were measured along the lines shown in the figure. The latter are the geographical lines of least resistance to dispersal above 2,500 m. The long central axis approximates the continental divide. The numbers that appear along the edges of this and other figures are degrees of south or north latitude and west longitude.

Additional specimens and behavioral observations of *brunneiventris* and *aterrima* in Peru were obtained during 7–18 August 1976 at 33 km NE Ingenio, 2,225 m, Department of Amazonas; 2–3 July 1976, Upper Rimac Valley, 3,050 m, Department of Lima; 4–8 August 1977, Cordillera Carpish, 2,600 to 3,200 m, Department of Huanuco; 12–21 October 1977 and 4–15 July 1978, Cerro Chinguela, 2,500 to 3,000 m, Departments of Piura and Cajamarca.

My analysis of the populations for possible introgression is based primarily on selected characteristics of the plumage: presence or absence of a pale superciliary line, humeral patch, and rufous malar mark; and color of the flanks, wing coverts, rump, breast, crissum and lower mandible. I did not use other plumage characteristics (e.g., size of the black throat patch in *brunneiventris* and intensity of feather pigmentation) because they were too variable due to fading and wear. Also, I did not use juveniles (because of their small size) or adults with unmolted immature or heavily worn plumage on the wings and tail in this study. In addition, I compared populations with respect to wing length (chord), tail length (from point of insertion of central rectrices to tip of the longest feather), tarsus length, and culmen length (from the anterior edge of the nostril). I compared certain population samples statistically using student's two-tailed *t*-test.

In the text, all taxa are referred to by their subspecific epithet (*nocticolor*, *humeralis*, *aterrima*, *brunneiventris*, *gloriosa*, *carbonaria*). The terms "hybrid" and "hybrid-like" are used to denote birds and character states thought to resemble the potential results of introgression or hybridization between the above taxa.

RESULTS AND DISCUSSION

PHENOTYPIC VARIATION OF *D. CARBONARIA* IN BOLIVIA

Published accounts of contact between *brunneiventris* and *carbonaria* in northwest Bolivia indicate that possible isolating mechanisms, acquired before secondary contact was established between the two taxa, were insufficient to prevent gene flow. Specimens showing intermediate characters and described as hybrids from the Department of La Paz have been known since the 1800's (Zimmer 1929). Based on collections of *brunneiventris* and *carbonaria* phenotypes during 1967–1968, in the Department of La Paz, Vuilleumier (1969b, unpubl. observ.) concluded that isolating mechanisms between the two taxa were incomplete and that a narrow zone of hybridization existed between them.

Through the courtesy of F. Vuilleumier, I examined the specimens that he collected in this zone of contact. In addition, I assembled a representative series of *carbonaria* pheno-

TABLE 2. Character index to score *carbonaria* phenotypes.

Character score	Rufous feathers on breast and abdomen	Malar mark	Length of superciliary line
0	None	None	None
1	Feathers with rufous edgings on lower abdomen	Trace of rufous on feather edges or gray feathers in malar areas	Trace only
2	Feathers with rufous edgings on abdomen and lower breast	Several rufous feathers on both sides	2 to 5 mm
3	Feathers with rufous edgings extensively distributed over abdomen and breast	Extensive rufous malar marks on both sides	>6 mm

types from the Departments of Cochabamba and Santa Cruz, the principal range of the taxon (Fig. 2). Then I used a modified "hybrid character index" (Anderson 1949) to test for possible introgression of *brunneiventris* characters in *carbonaria* phenotypes. Three characters often used for determining introgression were scored numerically with possible values ranging from 0 (for typical *carbonaria*) to 3 (typified by a hypothetical intermediate between *brunneiventris* and *carbonaria*; Table 2). Thus a "typical" *carbonaria* would score 0, whereas a hybrid exhibiting (a) extensive rufous malar marks (score 3), (b) a long superciliary line (score 3), and (c) extensive rufous feather edgings on the upper breast (score 3) would have a total score of 9. It should be noted that a pure *brunneiventris* (see Table 1) would also score 9. I scored these characteristics twice, at intervals of several days, to insure precision.

Although *brunneiventris* phenotypes have

TABLE 3. Character index scores for *carbonaria* in Bolivia.

Location	n	Average character index (maximum score = 9)	Individuals with "hybrid-like" characters (% of sample)	Estimated distance to nearest <i>brunneiventris</i> population ^b (km)
Caxata	9	0.33	33	0
Iquico	7	0.71	57	0
Palca ^a	4	0.25	25	25
Calacoto ^a	1	0.00	0	25
Tanapaca ^a	1	3.00	100	45
Chorros	7	0.57	14	135
Parotani ^a	1	1.00	100	215
Colomi	1	2.00	100	227
Incachaca	38	1.89	50	232
Tiraque	4	2.25	75	240
Chapare	5	0.80	60	250
Pocona ^a	11	0.64	55	293
Totora ^a	1	4.00	100	314
Aiquile ^a	3	1.00	33	342
Comarapa	9	1.89	67	360

^a Dry localities.

^b See Figure 2.

not been recorded east of the Rio de La Paz, I found specimens of *carbonaria* with "hybrid" characters from near the zone of secondary contact in the Department of La Paz eastward to near the limit of the species distribution in the Department of Santa Cruz. If introgression is responsible for these hybrid characteristics, one would assume that their frequency and intensity would be greatest near the zone of contact, and lower elsewhere. From the specimens at hand, however, the frequency and intensity of these characteristics are highest in samples from eastern populations far removed from possible sources of genetic contact with *brunneiventris* (Fig. 3, Table 3). Simplifying the data by deleting specimens collected from dry intermontane valleys (e.g., Calacoto and Aiquile) does not significantly change the relationship (Fig. 3). This suggests that factors other than introgression (e.g., pleiotropic and polygenic effects) are responsible for maintaining polymorphism in eastern Bolivian populations of *carbonaria*. Again, considering only these specimens collected on the Amazonian side of the continental divide, the average character index values increase clinally from northwest to southeast along the axis of the divide. Specimens collected in wet areas have a higher average character index value than birds from drier locales (1.43 vs. 0.86). However, there is no significant difference between the two groups in frequency of "hybrid" character expression (0.49 wet vs. 0.50 dry). A negative regression relationship would be expected if active introgression of *brunneiventris* genes was occurring in *carbonaria*.

The wet, humid conditions in temperate forests of central and eastern Bolivia (e.g., Incachaca) may favor certain coadapted gene combinations phenotypically expressed as "hybrid characters." If "hybrid-like" *carbonaria* phenotypes are the result of coadaptation to wet environments, then one would expect hybrid character indices in populations to change over a moisture gradient (i.e., from arid interior

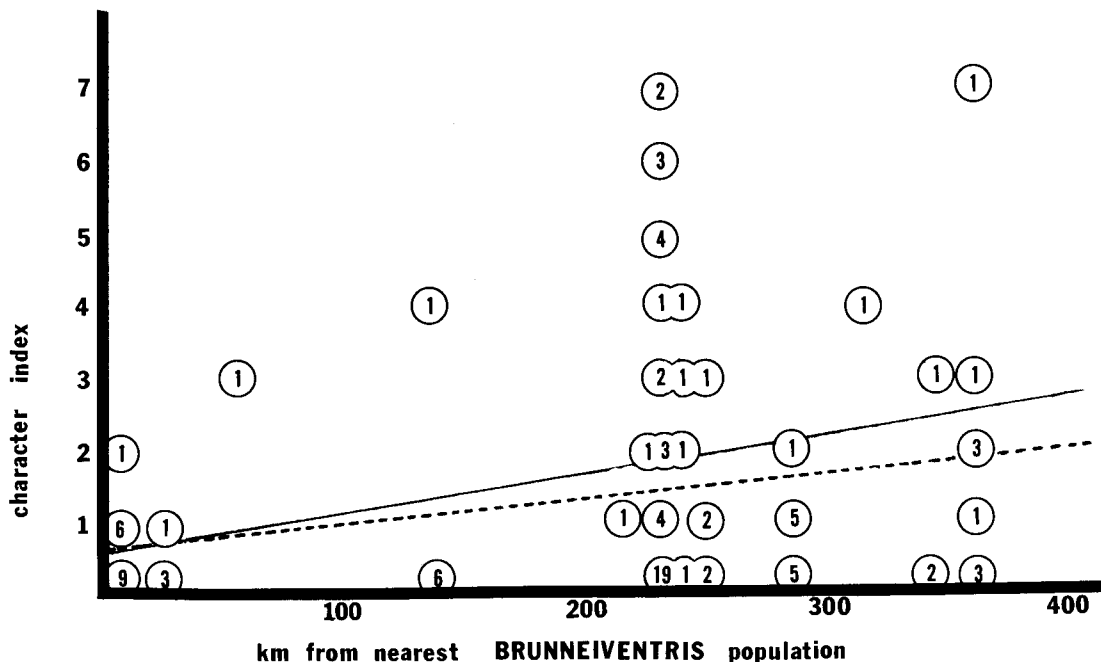


FIGURE 3. Relationships between character index scores of populations of *carbonaria* and the distance between them and the nearest population of *brunneiventris*. Sample sizes are in circles. The dotted regression line ($y = 0.600 + 0.004x$, $r^2 = 0.05$) describes the relationship for *carbonaria* from all localities. The solid line ($y = 0.520 + 0.005x$, $r^2 = 0.07$) describes the relationship for specimens from "wet" localities (see Table 3). The coefficient of determination of each line is statistically significant at $P < 0.05$.

valleys to the wet Amazonian slopes). Unfortunately, climatological data for the eastern slope of the Bolivian Andes are not available. Thus, precise correlations between rainfall and phenotype cannot be examined.

Endler (1977) maintained that populations can differentiate under a strong selection gradient despite extensive gene flow. The possibility that *brunneiventris* and *carbonaria* are exchanging genes, but retaining their phenotypic identity due to differential selection is questionable. In other parts of their ranges, *carbonaria* and *brunneiventris* inhabit a variety of ecotypes from dry chaparral to exceedingly wet *pajonal* and yet show no such gradient in phenotypic variability.

Birds with *D. carbonaria* phenotypes are regularly seen near and below the city of La Paz and in the dry shrubland of the foothills southwest of the continental divide (T. Parker and F. Vuilleumier, pers. comm.; Fig. 4). They also penetrate the high mountain passes of the Cordillera Hampaturi between Nevado Huayna Potosi and Nevado Illimani, where they may contact *brunneiventris*. The northwestern limits of *carbonaria* near La Paz coincide with the northwestern limits of the Bolivian dry intermontane avifauna (including Gray-hooded Parakeet, *Bolborhynchus ay-mara*; Red-tailed Comet, *Sappho sparganura*;

Rock Earthcreeper, *Upucerthia andaecola*; and Brown-backed Mockingbird, *Mimus dorsalis*).

The southeastern distribution of *brunneiventris* is limited by high mountains along the continental divide and by the drier valley of the Rio de La Paz, which is inhabited by *carbonaria*. It is perhaps not coincidental that hybrids between *brunneiventris* and *carbonaria* occur exclusively in or near a zone of ecological transition between relatively wet undisturbed forests on north-facing slopes of the Cordillera Hampaturi and drier, disturbed habitat covering the southeastern facing slopes overlooking the Rio de La Paz. The narrow zone between Chojlla (La Enramada) and Iquico where F. Vuilleumier (unpubl. observ.) collected hybrids of *brunneiventris* and *carbonaria* is no more than 10 km in width. Phenotypically "pure" populations of *brunneiventris* are found 30 km northwest of Chojlla at Hichuloma. Of the nine adult specimens that resemble *brunneiventris* and were collected at Chojlla by Vuilleumier, four are clearly hybrids between *brunneiventris* and *carbonaria*. These hybrids resemble *brunneiventris* with much enlarged, diffusely edged throat patches and reduced rufous malar marks. The other five specimens are indistinguishable from those in "pure" populations of *brunneiventris*. No *carbonaria* parental types

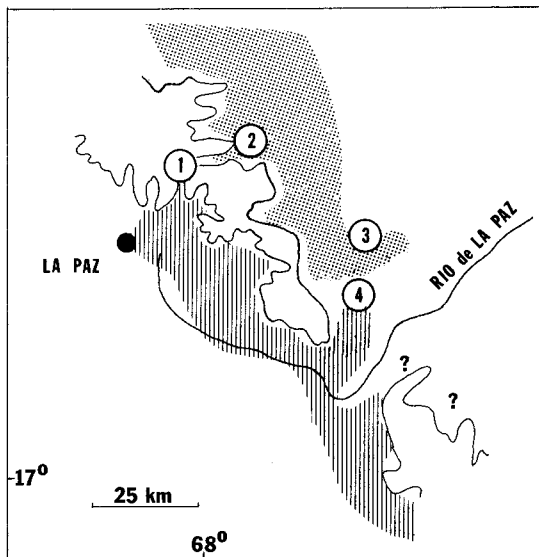


FIGURE 4. Zone of secondary contact between *brunneiventris* (stippled area) and *carbonaria* (hatched area) northeast of La Paz, Bolivia. Collecting localities: (1) Caxata, (2) Hichuloma, (3) Chojlla, (4) Iquico. Contour lines approximate 4,500 m. For location of this area, see Figure 1. Specimens have not been collected from areas designated by question marks.

have been collected at Chojlla, nor have they been seen there by F. Vuilleumier (pers. comm.). Another hybrid, perhaps the most intermediate specimen available (in the collection of the American Museum of Natural History; AMNH 793265), was collected 3 km from Iquico on the road to Mina Bolsa Negra. The seven specimens collected at Iquico are clearly *carbonaria* phenotypes. Vuilleumier (pers. comm.) describes the Iquico population as "essentially pure *carbonaria* . . . although with *brunneiventris* genes." However, some of the characters that he attributed to hybridization or introgression (e.g., a rufous-edged malar feather) may be natural variations in the phenotype of *carbonaria* as in eastern Bolivia. Away from the zone of contact, there are few indisputable signs of introgression between *carbonaria* and *brunneiventris*.

In the zone of contact, the differences in mensural characters between *carbonaria*, *brunneiventris*, and the Chojlla hybrid population are not significant (Table 4). This fact and the observed limits of the ranges of the two taxa suggest that competition prevents geographic overlap. Further study may show that although the breeding ranges of the phenotypes do not overlap, some non-breeding individuals occasionally stray into the range of their allopatric congener. The zone of secondary contact thus appears to be parapatric with little or no overlap of the parental phenotypes. Vuilleumier (unpubl. observ.) suggests that former barriers separating the taxa may have been modified by man, permitting secondary contact.

As a hypothetical alternative to present day introgression, the increased frequency of *brunneiventris* characters in eastern populations of *carbonaria* may be an "echo" of a proto-*carbonaria* genome delineated by a Cochabamba Pleistocene refuge. An echo is defined as the phenotypic expression of an allelic remnant of a genetically swamped population. During the pleniglacial period, a *brunneiventris*-like population of proto-*carbonaria* from an assumed Amazonia-facing refuge in Cochabamba may have been separated from a population restricted to the drier intermontane valley of the upper Rio Grande. In view of the wide ecological tolerance of present day *carbonaria*, it is plausible that proto-*carbonaria* stock survived in both a "wet" and "dry" refuge. The "two-refuge" hypothesis is partially supported by the concordance in ranges of a number of differentiated taxa that are restricted to dry montane steppe and forest edge (i.e., the Brown-capped Tit-Spintail, *Leptasthenura fuliginiceps*; Streak-fronted Thornbird, *Phacellodomus striaticeps*; and Creamy-breasted Canastero, *Asthenes dorbygni*) and the avifauna in the wet temperate forest of the Amazonian slope, typified by the Rufous-faced Antpitta (*Grallaria erythrotis*) and the Scimitar-winged Piha (*Chirocylla uropygialis*). These

TABLE 4. Measurements of *brunneiventris* and *carbonaria* from Bolivia.

	Locale ^a	Mean (mm) ± SE (n) of males			
		Wing	Tail	Tarsus	Culmen
<i>brunneiventris</i>	A	71.33 ± 0.70 (9)	61.25 ± 0.51 (10)	21.17 ± 0.21 (10)	7.70 ± 0.10 (11)
<i>brunneiventris</i> and <i>brunneiventris</i> × <i>carbonaria</i>	B	71.04 ± 0.60 (5)	60.44 ± 0.52 (7)	21.27 ± 0.21 (7)	7.90 ± 0.11 (7)
<i>carbonaria</i>	C	70.62 ± 0.81 (5)	60.56 ± 0.90 (5)	20.80 ± 0.29 (5)	8.07 ± 0.28 (3)
<i>carbonaria</i>	D	72.21 ± 0.53 (7)	62.16 ± 0.76 (8)	20.51 ± 0.32 (8)	7.65 ± 0.10 (8)

^a A = Hichuloma, Pongo, Unduavi; B = Chojlla (la Enramada) and 3 km NW Iquico; C = Iquico; D = Caxata.

wet and dry avifaunas probably differentiated in situ during the Pleistocene glaciations. The "dry" refuge population, derived and isolated from *brunneiventris*-like proto-*carbonaria*, lost part or all of the "ornate" characters of the ancestral stock (e.g., the rufous malar mark), and after the disappearance of barriers, genetically swamped populations of *carbonaria* in the "wet" Cochabamba refuge. Under these conditions, the present-day center of phenotypic variation in Cochabamba represents the remnant of former contact between two proto-*carbonaria* genomes now in equilibrium.

Selection between these alternatives is not possible without additional specimens from localities along climatic and geographic gradients.

THE ZONE OF SECONDARY CONTACT BETWEEN *BRUNNEIVENTRIS* AND *ATERRIMA* IN NORTHERN PERU

The existence of a zone of secondary contact between *aterrima* and *brunneiventris* in northern Peru has been suspected since the 1880's when these two taxa were reported near Cutervo, Department of Cajamarca (Zimmer 1929). Evidence of sympatry in the two taxa was obtained at Chira (near Tambillo), when two specimens of *aterrima* and one of *brunneiventris* were collected within a day of one another (see Bond 1955). However, the exact locations of "Chira" and "Tambillo" are unknown (Vaurie 1972) because there are several geographic features and communities within 20 km of Cutervo bearing these names. In the past, the distribution of *aterrima* and *brunneiventris* in this zone of contact has been documented primarily along roads (*aterrima*: between Huambos, Cochabamba, and Cutervo; *brunneiventris*: between Chota, Conchan, and Tacabamba). Vuilleumier (unpubl. observ.) recently narrowed the probable zone of contact between the two forms to the 30 km that separate the Huambos-Cutervo axis from the Chugur-Chota area. He (1969b, unpubl. observ.) concluded from available data and from field work in this zone of secondary contact during 1975 that *aterrima* and *brunneiventris* are reproductively isolated.

During field studies of *D. carbonaria*, I and other personnel from Louisiana State University Museum of Zoology (LSUMZ) collected 33 specimens of *brunneiventris* and 29 of *aterrima* from the zone of contact between Cutervo and Chota (Fig. 5). Our field work suggests that the ranges of *brunneiventris* and *aterrima* overlap slightly (parapatry), but that significant hybridization does not occur.

My field work in 1976–1978 indicated that the principal area of contact occurs from 3 to

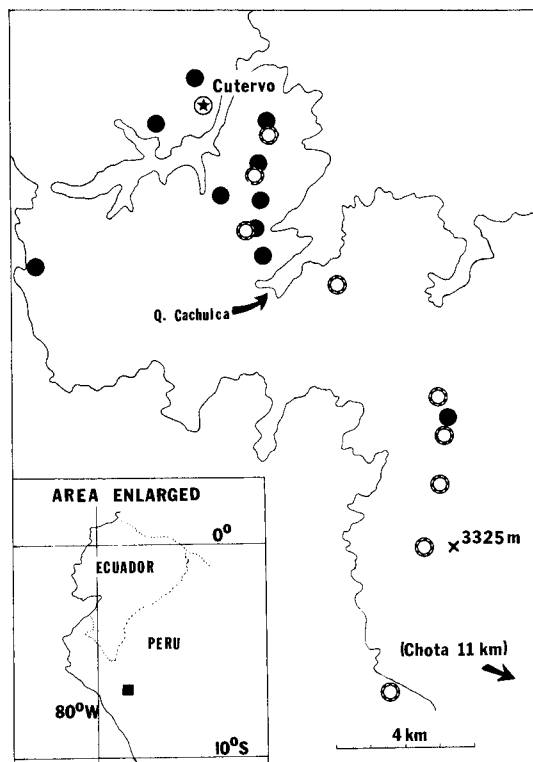


FIGURE 5. Region of secondary contact between *brunneiventris* and *aterrima* in the Department of Cajamarca, northern Peru. Collection sites are indicated by closed (*aterrima*) and open (*brunneiventris*) circles. The contour lines enclose areas above 2,600 m. For location of this region, see Figure 1.

7 km south-south southeast of Cutervo. (Contact between breeding populations of *brunneiventris* and *aterrima* is less likely to occur along the ridge south of the Rio Chotano between Huambos and Lajas because of low-elevation gaps [less than 2,400 m south of Cochabamba, Department of Cajamarca].) Except for a few hedgerows and plantings of *Eucalyptus* and *Alnus*, the terrain surrounding Cutervo is heavily cultivated. Consequently, habitat preferred by both phenotypes of *Diglossa* is patchy.

Near the North Peruvian Low (the lowest pass in the Andes between Venezuela and Chile), Carbonated Flower-Piercers inhabit shrubland and forest edge from about 2,400 m to timberline at 3,500 m. South of Cutervo this corridor of shrubland narrows to 3 km in width, thus bottlenecking the dispersal of *aterrima* and *brunneiventris*. The relatively dry, steep Quebrada Cachulca (upper Rio de Sucse), intrudes westward into this narrow corridor, further restricting dispersal and gene flow. In other words, contact between *aterrima* and *brunneiventris* is retarded by a combination of factors including (1) the patchiness of the habitat, (2) a partial geographic barrier,

and (3) the narrowness of the shrub zone linking them together.

I made a concerted effort to collect *brunneiventris* phenotypes encountered within the range of *aterrima* and vice versa. Of four *brunneiventris* collected (six seen) near Cutervo, two were adult females (LSUMZ 89184 and 89186), apparently mated to *aterrima* males. In both of the suspected "interspecific" pairings, I collected the female *brunneiventris* on the territory of a singing male *aterrima* with enlarged testes. One specimen (LSUMZ 89186) had a highly vascularized brood patch and the other (LSUMZ 89184) had slightly enlarged ova (2 mm). (I saw no other *brunneiventris* in the area, and intruding *aterrima* individuals from adjacent territories were vigorously chased.) Two days later, I also collected *aterrima* from areas adjacent to these singing males and the territorial singing males as well. None of them shows any signs of hybridization. Conclusive evidence of successful mating is lacking, however, since I did not find nests or young on these territories. I conclude that *brunneiventris* and *aterrima* may pair if potential mates of the appropriate phenotype are in short supply or not available.

Such "pairings" may indicate that male *aterrima* tolerate female *brunneiventris* because of interspecific ambivalence. However, my observations of intense inter-phenotypic aggression do not support this suggestion. In the zone of contact, *aterrima* and *brunneiventris* appear to occupy identical niches. I discerned no differences in the feeding behavior of the two taxa at clumps of flowering parasitic *Tristerix* (Loranthaceae) or in their interactions with hummingbirds. Furthermore, territorial male *aterrima* actively displaced non-territorial *brunneiventris* from *Tristerix* clumps and chased them to the borders of the territory.

A careful examination of the 26 specimens of *aterrima* and four *brunneiventris* collected immediately south of Cutervo revealed no obvious signs of hybridization (comparable to *brunneiventris* × *carbonaria* hybrids in Bolivia). In contrast to known hybrids of *D. carbonaria*, no *aterrima* exhibited rufous feather edgings on the malar areas, breast, belly, or crissum. Furthermore, the pale superciliary line, which is conspicuous in most specimens of *brunneiventris*, was absent in all of the specimens of *aterrima* that I examined, including those from the zone of secondary contact. (A few female *aterrima* have gray rumps and undertail coverts and resemble the most melanistic examples of *nocticolor* from the Santa Marta Mountains of northern Colombia. However, in the absence of other phenotypic

similarities, this variation cannot be directly attributed to introgression.)

The mensural characters of *brunneiventris* and *aterrima* from the zone of contact are not significantly different ([A and B] vs. C in Table 5). Such similarity in their morphological characters, as well as in their foraging behavior, suggests that competition prevents geographic overlap. However, non-breeding individuals of both phenotypes apparently wander into the range of their allopatric congener. Two specimens of *aterrima* (LSUMZ 85424: adult male, 11.5 km N, 2 km W Lajas, 2,800 m; LSUMZ 85416: subadult female, 7 km N, 3 km E Chota, 2,670 m) were collected 6 and 21 km, respectively, southeast of the nearest breeding population of *aterrima*.

That *aterrima* and *brunneiventris* interbreed occasionally is not surprising given their ecological circumstances. South of Cutervo the conditions for breakdown of isolating mechanisms appear to be ideal—disturbed and patchy habitat, and small breeding populations of the two taxa. Important in this discussion is the apparent absence of hybrids in the zone of phenotypic overlap. Long-term alteration of habitat in the zone of contact (Cutervo was founded in 1560) has had an unknown effect on the isolating mechanisms of the two taxa. Whether secondary contact has strengthened or eroded specific distinctness can only be determined by further study.

POPULATIONS IN THE NORTHERN ANDES

Of the seven recognized taxa of the *D. carbonaria* superspecies, five are found within a 500-km circle centered in northeastern Colombia (Fig. 6). The black populations, ranging from the Santa Marta Mountains in northern Colombia south to northern Peru, occupy a central geographic position in the array of rufous or gray-bellied polytypic forms.

Since its discovery in the early 1900's, the Colombian populations of *brunneiventris* have complicated interpretations of the origin and relationships of the superspecies. Occurring some 1,500 km north of the principal range of *brunneiventris* in Peru, the Colombian populations are apparently isolated in the northern ends of the Western and Central Cordilleras. After a careful examination of extant specimens, Zimmer (1929:26) stated "I am not able, therefore, to separate the Colombian and Peruvian birds [*brunneiventris*] even subspecifically except on the sole ground of geographic isolation, which is not adequate for racial distinction." Vuilleumier (unpubl. observ.) tentatively treats the Colombian *brunneiventris* as a member of a polytypic subspecies of the "*carbonaria* allospecies" on morphological

grounds, pending additional information on the evolutionary relationships of the group.

I examined 40 specimens of the Colombian *brunneiventris* from both sides of the Rio Cauca (i.e., from Páramo Paramillo, Páramo Frontino, and Hacienda Zulaiba), and found no phenotypic color characteristics that were consistently different from those of Peruvian *brunneiventris*. Although Zimmer (1929:25) stated that "the size of the Colombian specimens falls well within the range of variation of my Peruvian series," a mensural comparison of specimens from Colombia and the Chota-Cutervo region of Peru does reveal significant differences in some characters ([D and E] vs. [A and B] in Table 5). Several individuals superficially resemble hybrids of *brunneiventris* and *carbonaria* from Bolivia in having large diffusely-edged throat patches or disjunct malar stripes. However, many specimens of *brunneiventris* from Colombia cannot be visually discriminated from Peruvian specimens. In other words, the small populations of *brunneiventris* from Colombia appear to exhibit as much phenotypic variation as the widespread Peruvian populations. Whether this variability is due to introgression from nearby populations of *aterrima* or intrinsic genotypic variation is not known. In any case, the Colombian form warrants recognition at the subspecific level (Graves 1980).

Populations of the all-black form, *aterrima*, occur south of the headwaters of the Rio Porce on the Cerro de los Parados. The depression in the Andes (ca. 2,000 m) south of Medellín probably prevents extensive contact between *brunneiventris* and *aterrima*, but an overlooked population of either form may exist on either side of this gap.

A specimen of *aterrima* (in the collection of the United States National Museum; USNM

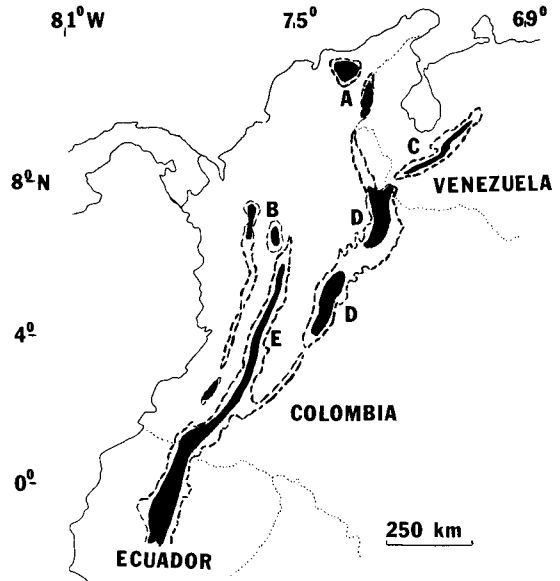


FIGURE 6. Current distribution of north Andean taxa of *Diglossa*: A = *nocticolor*, B = *brunneiventris* (*D. b. vuilleumieri*), C = *gloriosa*, D = *humeralis*, E = *aterrima*. The dashed lines denote elevations above 2,000 m (redrawn from Vuilleumier 1970a).

436793, with "juvenal" primaries) from Páramo Sonsón, Department of Antioquia, Colombia, has gray-tipped lesser wing coverts and a blackish-gray rump contrasting with a black lower back. Zimmer (1929) noted that several subadult specimens of *aterrima* from Laguneta, Department of Caldas, had gray-edged coverts. This may represent a trend in coloration toward the gray-shouldered *humeralis*. Unfortunately, a comprehensive series of adult *aterrima* from the northern end of the Central Cordillera is not available.

In the Eastern Cordillera, *humeralis* (a black

TABLE 5. Measurements of male *brunneiventris* and *aterrima*.

	Locale ^a	Mean (mm) ± SE (n)			
		Wing	Tail	Tarsus	Culmen
<i>brunneiventris</i>	A	68.14 ± 0.55 (8)	58.44 ± 0.88 (7)	21.14 ± 0.18 (8)	8.08 ± 0.15 (8)
<i>brunneiventris</i>	B	68.19 ± 0.66 (8)	58.90 ± 0.90 (7)	21.39 ± 0.14 (8)	8.29 ± 0.10 (8)
<i>aterrima</i>	C	69.61 ± 0.61 (7)	60.63 ± 0.68 (7)	21.16 ± 0.21 (7)	8.20 ± 0.24 (6)
<i>brunneiventris</i>	D	66.56 ± 0.62 (11)	57.88 ± 0.73 (12)	20.48 ± 0.16 (12)	7.88 ± 0.11 (12)
<i>brunneiventris</i>	E	66.60 ± 0.51 (6)	57.93 ± 0.59 (6)	20.12 ± 0.20 (6)	7.58 ± 0.26 (5)
	<i>P</i> ^b	0.02	NS	0.001	0.01

^a A = Cutervo-Lajas transect; B = 7 km N, 3 km E Chota; C = Cutervo; D = Paramillo-Frontino; E = Hacienda Zulaiba.

^b Measurements of A versus B and D versus E are not significantly different ($P > 0.05$). The pooled values (A + B vs. D + E) were compared using a two-tailed Student's "t" test; the *P* values in the table are for these comparisons. Pooled measurements of *brunneiventris* (A + B) are not significantly different ($P > 0.05$) from the measurements of *aterrima* (C).

race with gray rump and shoulders) ranges from south of Bogotá north to the Department of Norte de Santander. The gap between the *humeralis* populations shown in Figure 1 is probably due to the lack of collecting, because the Eastern Cordillera from Bogotá northward to Venezuela is generally above 3,500 m in elevation. South of Bogotá, several elevational gaps (ca. 2,000 m) now prevent contact between *humeralis* and *aterrima* along the Eastern Cordillera. To the north, the Táchira Depression separates the *humeralis* population on Cerro de Tamá from *gloriosa* in the Táchira Andes (Vuilleumier, unpubl. observ.).

In *humeralis*, the extent of gray on the humeral area and rump is variable, with the darkest individuals resembling *nocticolor* (e.g., USNM 374838, Pamplona, Department of Norte de Santander). I examined a series of *humeralis* for signs of introgression from neighboring "rufous" taxa. Of 65 adult specimens, 11 exhibit either a pale superciliary line or rufous feathers in the crissum (one "Native Bogotá" specimen; one from Norte de Santander; four from Santander; one from Boyacá; four from Cundinamarca). In USNM 470509 (Chía, Sabana de Bogotá), the feathers of the crissum have gray centers and broad rufous borders. In a situation analogous to the occurrence of "hybrid-like" *carbonaria* in eastern Bolivia, these specimens of *humeralis* from scattered locales up to 250 km from the nearest "rufous" populations do not seem to be the products of introgression. No rufous was found on the belly, breast, or malar areas in *nocticolor*, *humeralis*, or *aterrima*. However, in common with occasional individuals of *nocticolor* and *aterrima*, several of the *humeralis* specimens have faint gray barrings on the flanks, upper tail coverts, crissum, and lower belly.

Paynter (1978) suggested that in addition to the north Andean refuges proposed by Haffer (1969, 1974), the western slope of the Nevada del Cocuy (the highest peak of the Eastern Cordillera) may have served as a refuge. A persistent "rufous" refugial population on the western slope of the Eastern Cordillera may have been swamped during the northward dispersal of black "*aterrima*-like" birds from the Napo refuge (eastern Ecuador). The observed phenotypic variation in *humeralis* may again be an "echo" of former contact between the two gene pools. An alternative but less satisfactory hypothesis is that introgression from nearby *gloriosa* is responsible for "hybrid-like" characters.

The gray-rumped form, *nocticolor*, occurs in the Serranía de Perijá and Sierra Nevada de Santa Marta. Zimmer (1929) noted that some

specimens of *nocticolor* resemble those of *humeralis* in having gray tips on the upper wing coverts, thus bridging the difference between typical *nocticolor* and *humeralis*. I examined 105 adult *nocticolor* and found that the percentage of specimens having gray feathers in the humeral area was lowest in the northwesternmost populations (San Lorenzo), i.e., those farthest removed from populations of *humeralis* (see Table 6). All available specimens from Serranía de Perijá have at least some trace of gray edgings on the upper wing coverts, although none have humeral patches as extensive as those typical of *humeralis*.

The black-and-rufous (chestnut) form, *gloriosa*, of the Venezuelan Andes is intermediate in many characters between the black subspecies, *humeralis* and *brunneiventris*. Vuilleumier (1969b) noted that many individuals of *gloriosa* with rufous malar spots resembled hybrids of *brunneiventris* and *carbonaria* from Bolivia. In the present study, 21 of 25 adult specimens from scattered localities show traces of rufous malar spots. Since *gloriosa* is geographically isolated from other forms of *Diglossa*, presumably these hybrid-like characteristics are not due to ongoing genetic infiltration from nearby black populations. This suggests that the "rufous" population (*brunneiventris*-like) of the Venezuelan Andes was contacted by the black proto-*humeralis* across the Táchira Depression during the glacial lowering and expansion of the Andean forest. Assuming that isolating mechanisms had not developed at the time of contact, hybridization was uninhibited. Gene frequencies subsequently reached equilibrium during the present interglacial isolation.

HYPOTHETICAL SCHEME FOR SPECIATION IN THE *DIGLOSSA CARBONARIA* SUPERSPECIES

Using existing geographic distribution and phenotypic characteristics of populations and geo-historical events, zoogeographers can reconstruct putative speciation models (Vuilleumier 1981b). These models are difficult or impossible to test, but I propose the following as a nucleus for experimentation. In attempting to reconstruct the evolutionary history of the *D. carbonaria* superspecies, several less likely hypotheses may be rejected in favor of a "best-fit" hypothesis of speciation consistent with the Pleistocene history of the Andes (but see Dunbar 1980).

The ancestral stock of the *D. carbonaria* complex probably evolved in northwestern South America, the present center of distribution of the genus. During the general uplift of the Andes in the late Pliocene and early

Pleistocene, proto-*carbonaria* stock probably adapted to the newly formed shrublands in the temperate zone. Diglossine stock from the pre-existing South Venezuelan Highlands may have invaded the emerging Andes. Mayr and Phelps (1967) proposed that *D. duidae* of the Venezuelan Tepuis is the product of an invasion of the flower-piercers from the Andes and is related to *D. carbonaria*. Vuilleumier (1969b) considered *D. duidae* to be related to either the *lafresnayii* or the *carbonaria* superspecies. Since the Venezuelan Highlands predate the Andes, it is possible that the Andean *carbonaria* and *lafresnayii* superspecies were products of a double invasion from the Venezuelan Highlands. The geographic distribution and partially overlapping phenotypic complexes of the *carbonaria* and *lafresnayii* superspecies may indicate that they are undergoing a process similar to the "taxon cycles" that occur on islands (Wilson 1961). However, this interesting possibility cannot be verified without a thorough study of speciation in the *lafresnayii* superspecies.

Following their adaptation to the emerging temperate zone shrubland, groups of flower-piercers may have spread southward along the Andean chain to about 20°S latitude (i.e., to the current southern distributional limit of the *D. carbonaria* superspecies in the Department of Chuquisaca, Bolivia; Fig. 1). Examination of present distributions of the superspecies suggests that the ancestral taxon resembled the present-day form *brunneiventris*, which now has two isolated relictual populations at the northern end of the Western and Central Cordilleras of Colombia some 1,500 km north of its extensive Peruvian range (Fig. 1). This distributional pattern suggests that the formerly continuous range of the *brunneiventris*-like (rufous-bellied) proto-*carbonaria* was fragmented so that groups are now separated by the black form *aterrima* in Colombia, Ecuador, and Peru.

It is not known if proto-*carbonaria* was isolated in North Andean glacial refuges before its Andes-wide dispersal. However, during the first major glacial period following its dispersal, proto-*carbonaria* was probably isolated in a number of highland refugia along the eastern slope of the Andes (Fig. 7). A myriad of other less persistent, smaller, and isolated refuges also probably existed in moist forest pockets at the heads of river valleys on the eastern slope and to a lesser extent on the western slope. Some differentiation probably occurred in these transient refugia, which were obliterated during the climatic extremes of glacial cycles. The rufous-breasted "ornate" proto-*carbonaria* of the Napo and Cocha-

TABLE 6. Gray coloration in the humeral area of *noc-ticolor*.

Location	n	Individuals with gray-tipped lesser wing coverts	Individuals showing gray in humeral area (% of sample)
San Lorenzo	13	5	38
Paramo de Churuqua	10	6	60
Paramo de Macotama	29	21	72
San Miguel	6	3	50
Rio Guatapuri	9	7	78
Mamancanaca	4	3	75
Siminchucua	8	7	88
Chirua	3	3	100
Sierra Perijá (South Teta)*	6	6	100
Laguna de Junco*	11	11	100

* Serrania de Perijá.

bamba refuges apparently underwent a series of progressive or sudden melanic phenotypic changes, either through natural selection or genetic drift.

There is ample evidence of widespread Pleistocene volcanism in the northern Andes (see Folster and von Christen 1977, Folster et al. 1977, and Folster and Hetsch 1978). The deposition of successive layers of volcanic ash between 32,000 and 10,000 years B.P. in the Western, Central, and Eastern Cordilleras of Colombia and adjacent Ecuador, darkened the shrubland and cloud forest. One can imagine microphyllous timberline cloud forest hundreds of kilometers from the centers of volcanic activity covered with precipitating ash. Chapman (1926) cautiously suggested that central Andean populations of *brunneiventris* were devastated by volcanic activity, thus allowing a new form (*aterrima*) to fill the distributional void. In the Napo refuge, the mutation of the "ornate" proto-*carbonaria* to a melanistic form, which matched the environment more closely, could have been stabilized rapidly by natural selection. The preponderance of high Andean taxa exhibiting dull gray, brown, and black plumage probably is not coincidental (e.g., *Cinclodes*, *Scytalopus*, *Turdus*, *Diglossa*, *Phrygilus*, *Catamenia*). Of the 38 north Andean passerines listed by Vuilleumier and Simberloff (1980: Appendix 7), only the Eastern Meadowlark (*Sturnella magna*) and the Andean Siskin (*Spinus [Carduelis] spinescens*) (both with yellow underparts) are brightly colored. Johnson and Brush (1972) suggested a similar selective advantage in dark color morphs of *Chlorospingus* from the volcanic highlands of Costa Rica. In contrast, the incomplete melanization of *carbonaria* in the Cochabamba region of Bolivia may be unrelated to volcanism.

As periods of glaciation began and cooler

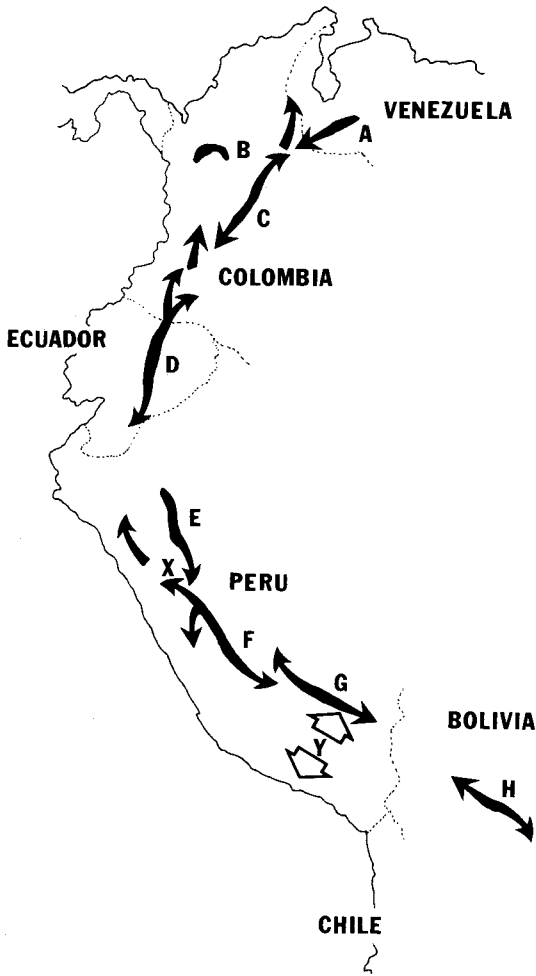


FIGURE 7. Areas proposed as major refugial centers of differentiation for high Andean birds inhabiting wet temperate areas during arid parts of the middle-to-late Pleistocene Period. A = Venezuelan Andes, B = Nechí, C = Magdalena?, D = Napo, E = Huallaga, F = Junin, G = Cuzco, H = Cochabamba. Refuges B, D, and the "Eastern Peruvian Refugia" (E, F, G) were probably confluent with the lowland refuges of Haffer (1974). Other smaller and less effective potential refuges (including the Sierra Nevada de Santa Marta, Serranía de Perijá, and Central Cordillera of Colombia; the upper and lower Marañón, upper Apurimac, and Tarija of northwestern Argentina) are not depicted. Arrows depict repetitious routes of dispersal from refugial areas during the onset of glaciation. Suture zones should be detected between major refuges, provided that no smaller refuges occupied the intervening territory. The upper Marañón corridor (X) is the major dispersal route between the eastern and western slopes of the Central Andes in Peru. *Polylepis* wood land at the head of river valleys (Y) probably formed important dispersal bridges ("islands") across the northern Altiplano in central and southern Peru during interglacial periods.

climatic conditions prevailed, temperate vegetation retreated from the highlands and alpine vegetation became more extensive, i.e., advanced to lower elevations. This probably permitted high Andean birds to disperse rather

freely and populations of *carbonaria* from several of the less widely separated refuges (e.g., the three Peruvian refuges in Fig. 7) came into contact with each other. However, during peaks of glaciation, the climate was extremely dry (Van der Hammen 1974) and the size of habitable areas again shrank, restricting dispersion and gene flow between these groups of birds (Graves, unpubl.), even though some highland refugia probably remained confluent with nearby lowland refugia (Haffer 1974). It is probable that the Bolivian refuge remained isolated, perhaps blocked by the extensive glacial formation east of present day Lake Titicaca. B. Vuilleumier (1971) hypothesized that glaciers and tongues of ice created enough of a gap in the puna vegetation east of Titicaca to have caused divergence of populations on either side of it.

The melanistic Napo group in Ecuador (D in Fig. 7) expanded northward into Colombia and invaded the southern portion of the Western Andes, as well as the Central Andes. The "rufous" *carbonaria* of the Venezuelan (Mérida) refuge (A in Fig. 7) was relatively isolated from the Colombian Andes by the Rio Torbes Valley which acts as a filter barrier. However, it is probable that during the humid, but cool climatic conditions at the beginning and end of glacial periods, when temperate vegetation retreated and high Andean forest was more extensive, gene flow across this barrier was considerable. The Serranía de Perijá and the Sierra Nevada de Santa Marta in Colombia did not uplift until the late Pleistocene (B. Vuilleumier 1971) and probably underwent only one glaciation. In the Western Cordillera, habitat islands fluctuated greatly in size during glacial cycles, apparently leading to the extinction of either black or rufous forms of *carbonaria* in the Departments of Cauca and Antioquia in Colombia. Melanistic stock from the Eastern Cordillera (C in Fig. 7) probably dispersed northward during the last glacial cycle, contacting the rufous population of the Mérida refuge. The rufous *carbonaria* on the Nechí refuge (at the northern end of the Western and Central Cordilleras; B in Fig. 7) remained isolated during this period.

The last glacial extreme again isolated various taxa of *carbonaria* in refugial areas that probably lie within their current ranges. These groups subsequently became phenotypically distinct and developed isolating mechanisms within these refuges, probably during the Late Pleistocene and Holocene. More recently, in the last 8,000 to 10,000 years, amelioration of climatic conditions has allowed secondary contact between several of them (*brunneiventris* and *aterrima* in northern Peru, and *brun-*

neiventris and *carbonaria* in northwestern Bolivia; see Fig. 1).

The validity of this model of speciation may be tested by comparing the distribution of *Diglossa* and other birds that inhabit forest and shrubland in the high Andes and have similar dispersal capabilities.

TAXONOMIC CONCLUSIONS

On the basis of existing information, I believe that the *D. carbonaria* superspecies consists of three or possibly four allopatric or parapatric taxa at or near the species level. The black forms, *nocticolor* and *humeralis*, are very closely related and only subspecifically distinct. The entirely black *aterrima* is a well-marked subspecies of *D. humeralis*, which thus includes *nocticolor*, *humeralis*, and *aterrima*. The forms *brunneiventris* and *carbonaria* hybridize only in a narrow zone of overlap in northwestern Bolivia. Assuming the existence of "partial" isolating mechanisms between the two taxa, they should be treated nomenclaturally as semispecies (taxonomic species *in sensu* Short 1969). The Colombian population of *brunneiventris* is subspecifically distinct from Peruvian *brunneiventris*. The Venezuelan form *gloriosa* is a distinct allospecies related to both black and rufous forms.

DIGLOSSA CARBONARIA SUPERSPECIES

- I. *humeralis* allospecies (*D. humeralis*)
 - subspecies—*humeralis* (*D. h. humeralis*)
 - subspecies—*nocticolor* (*D. h. nocticolor*)
 - subspecies—*aterrima* (*D. h. aterrima*)
- II. *brunneiventris* allospecies (*D. brunneiventris*)
 - subspecies—Peruvian form (*D. b. brunneiventris*)
 - subspecies—Colombian form (*D. b. vuilleumieri*)
- III. *carbonaria* allospecies (*D. carbonaria*)
- IV. *gloriosa* allospecies (*D. gloriosa*)

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RECENT PUBLICATIONS

Annotated Checklist of the Birds of Arizona. Second Edition/Revised and Expanded.—Gale Monson and Allan R. Phillips. 1981. University of Arizona Press, Tucson. 240 p. Paper cover. \$5.95. This authoritative checklist is the revised edition of a work first published in 1964. Documented species are distinguished from hypothetical species. The entry for each species gives its seasonal and distributional status, the subspecies represented, and a summary of important records, especially in the past 20 years. An appendix gives a special discussion of the races of the Red Crossbill (*Loxia curvirostra*) in Arizona, including descriptions of two new subspecies. This pocket-size book will be an indispensable field reference for serious birders in Arizona. Index.

The Birds of Northeastern Utah.—William H. Behle. 1981. Occasional Publication No. 2, Utah Museum of Natural History, University of Utah, Salt Lake City, Utah. 136 p. Paper cover. \$10.95. This work supplements Behle and Perry's comprehensive *Utah Birds* (noted in *Condor* 77:371), being a detailed report on the hitherto little-known avifauna of the northeastern part of the State. A long introduction presents several aspects of the area, its ecology, and its birdlife. Several tables summarize information on habitat usage and density of hawks and owls. The species accounts cover seasonal status, ecological occurrence, a summary of specimens obtained, other pertinent localities where the species was seen, and a resumé of previously published records. For some species there are remarks on natural history and/or systematics. A list of references is given, but regrettably no map. Although this book will be useful to serious birders, it is primarily intended for curators and researchers who are working on the distribution and taxonomy of birds in Utah and adjacent states.