

DISTRIBUTION PATTERNS AND ZOOGEOGRAPHY OF *ATLAPETES* BRUSH-FINCHES (EMBERIZINAE) OF THE ANDES

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ABSTRACT.—We attempted to determine why the distribution of *Atlapetes rufinucha* (Rufous-naped Brush-finch; Emberizinae) is so patchy. This common, sedentary species is found in several discrete areas of the humid Andes separated by distances of hundreds of kilometers, yet the gaps contain seemingly suitable habitat. Mapping of 906 specimen localities by both latitude and elevation shows that these gaps are filled by populations of other *Atlapetes* species, especially *A. tricolor* and *A. schistaceus* (a gray-plumaged species currently thought to be only distantly related to *rufinucha*, a species with yellow-and-green plumage), which in turn also show complementary, patchy distributions. Where *rufinucha* is the only species found, it occupies the entire elevational gradient. Where two or more species occur, their elevational distributions are restricted and often complementary. We attribute these patterns to interspecific competition. Hypothetical reconstructions of the sequence of historical events that would generate such a checkerboard distribution pattern in these sedentary taxa are complex. A novel hypothesis that would greatly simplify historical reconstructions is that *rufinucha*, *schistaceus*, and perhaps *tricolor* refer only to recurring color patterns characterized by differing amounts of pigment in the feathers and, therefore, adjacent populations (regardless of current taxonomic designation) are more closely related than either is to more distant populations of the same "species." Therefore, *rufinucha* and *schistaceus* populations would be merely allopatric forms of the same lineage that alternate in color pattern (yellow or gray) between adjacent populations, as known for three other lineages of Andean birds. We found limited support for such a hypothesis. Even if *rufinucha* and *schistaceus* are distinct species, we predict that they are much more closely related than currently believed and that they differ primarily in pigment concentration. The dramatic differences in phenotype created by differences in pigment concentration in the plumage may frequently cause problems for phenotype-based taxonomic hypotheses. Received 22 December 1992, accepted 12 May 1993.

DETERMINING WHY A SPECIES is limited to a particular geographic area is one of the most difficult questions in bird ecology. The reason for this difficulty is that finding the answer requires a knowledge of the complex influence of history on current ecology (Vuilleumier and Simberloff 1980). Furthermore, even if potential limiting factors can be identified from this knowledge, experimental manipulation of these variables is virtually impossible (Diamond 1986). Nevertheless, analyses of comparative distribution patterns may be used to test certain hypotheses concerning the determinants of the limits of distribution (e.g. Remsen and Cardiff 1990).

The unusual geographic distribution of *Atlapetes rufinucha* (Rufous-naped Brush-finch;

Emberizinae) naturally provokes the question: Why is the distribution so patchy? Several disjunct populations are distributed in the Andes from northern Colombia and Venezuela south to central Bolivia, with some populations isolated by as much as 300 km from their nearest conspecifics (Paynter 1978, Graves 1985; Fig. 1). Because *A. rufinucha* is a nonmigratory species with short, rounded wings that seem unlikely to propel the bird more than a few meters at a time, we believe that past episodes of long-distance dispersal are unlikely to explain the disjunct populations; therefore, we assume that vicariance is responsible for the present disjunctions.

Because the gaps in distribution of *A. rufinucha* contain the same general habitat currently supporting the species, namely montane forest edge, it seems unlikely that distributional gaps are caused by habitat unsuitability or other autecological factors. In fact, habitat differences along the elevational gradient within areas in-

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habited by *A. rufinucha* appear to be much greater than those between similar elevations within and outside its latitudinal range. The distribution of most Andean birds is much more sensitive to changes in habitat associated with elevation than latitude (Chapman 1917, 1926), and most species have remarkably similar elevational distributions throughout their latitudinal range (Remsen and Cardiff 1990), particularly when differences in slope are taken into account and when records of wandering individuals are excluded (Graves 1985). Therefore, we think that habitat differences do not influence the presence of gaps in distribution.

Another potential influence on the distribution of *A. rufinucha* might be competition from the large number of congeners in the Andes (Paynter 1978). If interspecific competition determines the limits of distribution of *A. rufinucha*, then the gaps in its distribution should correspond to areas where similar *Atlapetes* species are present. To test this prediction, we mapped the latitudinal and elevational distribution of other species of *Atlapetes* in the Andes.

Although Paynter (1978) previously mapped latitudinal distributions of all Andean species using collecting localities, he was unable to map elevational distributions because such data were largely lacking. Paynter proposed that the patchy distribution of *A. rufinucha* was caused by interspecific competition, but without the added dimension of elevation, the complementarity in distributions was difficult to assess. However, with the recent completion of the gazetteers organized by Paynter for all of the Andean countries (Paynter et al. 1975, Paynter and Traylor 1977, 1981, Paynter 1982, 1985, Stephens and Traylor 1983), mapping elevational distributions is now feasible. Furthermore, 15 years of additional fieldwork since Paynter (1978) has generated much additional locality data, particularly in Peru and Bolivia.

Sixteen currently recognized species of *Atlapetes* inhabit forest and scrub in the Andes of South America from the lower limit of montane vegetation to timberline (Meyer de Schauensee 1966, Paynter 1970, 1978). Of these, two species, *torquatus* and *brunneinucha*, are large in size and more strictly terrestrial, and were formerly placed in their own genus, *Buarremon*. Hackett (1992) found that these species are distantly related to other *Atlapetes* and that *Buarremon* should be resurrected for them. Thus, their distribution patterns are analyzed separately, and they are

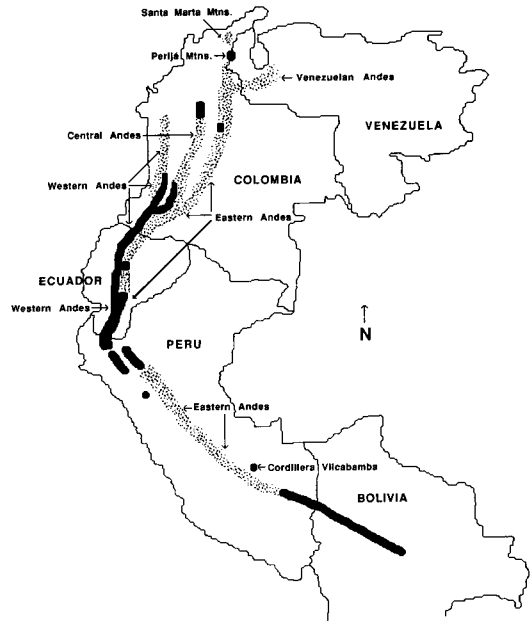


Fig. 1. Schematic representation of disjunct distribution of *Atlapetes rufinucha* in montane western South America. Blackened areas represent areas where *A. rufinucha* occurs, whereas stippled areas represent montane regions with humid forest where it does not occur.

syntopic with the *Atlapetes* species treated herein throughout their geographic ranges (Remsen and Graves 1995). Paynter (1978) proposed that the remaining *Atlapetes* species fall in three different lineages based on plumage characters: (a) the *schistaceus* group (including *schistaceus* and *leucopterus* of the humid Andes), those species with primarily gray plumage; (b) the *pileatus* group (including *rufinucha*, *melanocephalus*, *albifrenatus*, *leucopis*, *flaviceps*, *fuscoolivaceus*, *tricolor*, *fulviceps*, *semirufus*, and *citrinellus* of the humid Andes), those species with predominantly yellow underparts and unicolored crown patches; and (c) the *albinucha* group (including *gutturialis* and *pallidinucha* of the humid Andes), those species with bicolored crowns.

METHODS

We gathered specimen localities from major museums for all *Atlapetes* species that occur on the humid slopes of the Andes Mountains from northern Venezuela and Colombia to northern Argentina. We included the Perijá Mountains of northern Colombia and Venezuela as an extension of the Eastern Andes.

The Santa Marta Mountains of Colombia were treated separately. We also treated the Andes of Venezuela separately; for simplicity, we included in this region both the extreme eastern edge of the Eastern Andes in southwestern dept. Táchira and the somewhat isolated Cordillera de Mérida, an extension of the Eastern Andes into western Venezuela, even though these areas are separated by a gap in suitable high-elevation habitat (Vuilleumier 1971, Vuilleumier and Ewert 1978). We did not treat areas of the Andes where some *Atlapetes* species occur, but where the predominant vegetation was not humid forest (e.g. western slope of Western Andes at low elevations in southwestern Ecuador and northwestern Peru; Western Andes of most of Peru; and most of western slope of Eastern Andes of Peru).

Latitudes were taken primarily from the ornithological gazetteers of the Andean countries (for list, see Introduction). Following the methodology of Remsen and Cardiff (1990), if a specimen label did not include elevation, the gazetteers were used to determine whether the elevation could be ascertained with reasonable precision. Many specimen localities could not be used because their elevations were uncertain. Localities that differed in elevation by less than 25 m were treated as the same locality.

Use of specimen localities to determine distributions has drawbacks. First, specimen localities obviously represent a conservative estimate of distribution; however, no acceptable alternative exists for Andean birds, whose distributions are known primarily from collections. Fortunately, collectors have managed to penetrate most areas of this region, one renowned for difficult access and working conditions. Second, older collecting localities often represented base camps from which collectors ranged up- and down-slope, yet all specimens were frequently given the same elevation, the elevation of the camp (e.g. see Paynter 1978). Even at recent localities, differences of 25 to 100 m in elevation among specimens may not be reflected in their label data. Thus, use of specimen localities overestimates true overlap in elevational distribution. Third, if two or more species of *Atlapetes* were collected at the same locality, differences in habitat or slope would have been recorded only on the most recent specimen labels. A fourth disadvantage, namely that collectors might miss one or more species at a locality, is minimized for *Atlapetes* brush-finches, which are usually among the most common and conspicuous birds at Andean forest localities, and their preference for forest edge near the ground makes them readily collected with mist nets or shotguns.

A drawback of our mapping technique is that use of latitude-by-elevation plots assumes that only one slope faces away from the highest elevations in a given mountain range. In reality, few places have a single, long slope from timberline to lowlands. Instead, most areas are much more complex topograph-

ically, with series of parallel ridges and spurs that may produce rain shadows that in turn may affect habitat and bird distribution. Therefore, our figures represent only first approximations of general patterns and cannot reveal important local heterogeneity. Thus, our technique again overestimates true overlap. Only careful fieldwork on a local scale can determine the degree to which our technique overlooks real differences in distribution. Also, where the Andes run nearly east-west instead of north-south, such as in northern dept. Cuzco, Peru, a simple plot of elevation by latitude will also overestimate true overlap.

RESULTS

Eastern Andes (eastern slope).—On the eastern slope of the Eastern Andes of Peru and Bolivia, the gaps in the range of *A. rufinucha* are filled to varying degrees by another *Atlapetes* species (Figs. 2 and 3). The southernmost species, *A. citrinellus*, occupies a broad range of elevations in northern Argentina from about 28°00' to 23°36'S. Although *A. citrinellus* and *A. fulviceps* overlap in the provinces of Jujuy and Salta, they evidently have not been collected at the same locality, with *citrinellus* generally occupying only lower elevations. From the northern limit of *A. citrinellus* to central Bolivia, *A. fulviceps* occupies most elevations. Its latitudinal distribution overlaps slightly with that of *A. rufinucha* in depts. Cochabamba and La Paz, Bolivia, but *A. fulviceps* is restricted to drier woodlands (Remsen et al. 1988, Fjeldså and Krabbe 1990, T. A. Parker pers. comm.) and is not known to be syntopic with *A. rufinucha*. The latter is found from central Bolivia north to the Urubamba River valley of southern Peru. Paynter (1978) could not be certain that the lengthy gap was real between these populations of *A. rufinucha* and the next one to the north in northern Peru. With extensive fieldwork there since then, we can now be certain that the gap is present and that it is filled neatly by two species, *A. schistaceus* at high elevations and *A. tricolor* primarily at low elevations. These two species extend from the Urubamba Valley at about 13°S north to about 8°S, in dept. La Libertad, Peru. From there north to about 3°S in Azuay province, Ecuador, *A. rufinucha* is the only species except for *A. pallidinucha* (at a few high-elevation localities) and *A. leucopterus paynteri* (Fitzpatrick 1980), a humid-forest representative of a species typically found in drier habitats, at two lower-ele-

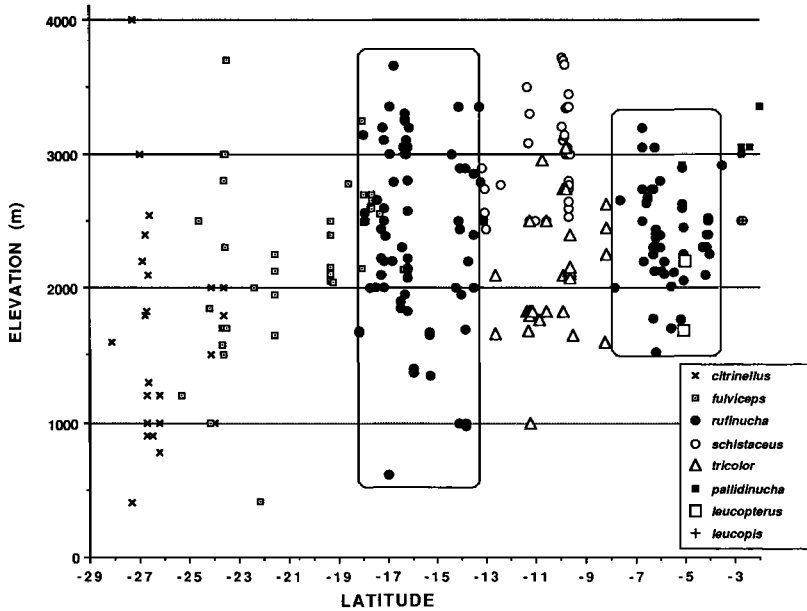


Fig. 2. Distribution of eight species of *Atlapetes* on eastern slope of Eastern Andes from northern Argentina to central Ecuador. Each point represents locality from which one or more specimens of species obtained. Boxes enclose areas where *A. rufinucha* found. On this and other figures, we use convention that negative values indicate degrees south latitude, and positive values, degrees north latitude. In this and other regions (covered in Figs. 3–9), lower limit of montane cloud forest usually about 1,200 to 1,300 m, and upper limit about 3,300 to 3,400 m. There is area from about 7° to 9°S in Peru that seems to be missing a high-elevation *Atlapetes*; in contrast to other gaps caused by insufficient sampling, this area in depts. San Martín and La Libertad has been surveyed intensively at several localities. Not included in this figure is Cordillera Vilcabamba in dept. Cuzco, Peru, at 12°36'S, an isolated spur of Andes where *A. rufinucha* recorded from 2,520 to 3,520 m, and *A. tricolor* at 2,100 m (Weske 1972); the *rufinucha* population there, a new subspecies (*A. r. terborghi*; Remsen 1993), is northernmost of species in this region and occurs north of *A. schistaceus* in nearby main Andes.

vation localities, all in dept. Cajamarca, Peru. From central Ecuador to the Andes of northern Colombia (Fig. 3), six species of *Atlapetes* are found, with little consistent elevational or latitudinal segregation. In this extensive area, *A. rufinucha* has been found at only two localities, both just north of the equator in Ecuador. In the Perijá Mountains, *A. rufinucha phelpsi* is known from elevations below and *A. schistaceus* from those above about 2,300 m.

Of 384 localities on the eastern slope of the Eastern Andes, only a single species of *Atlapetes* has been collected at 374 (97.4%) and two species at only 10 (2.6%). South of the Marañón River, two species have been collected together at only two localities, both involving *A. schistaceus* and *A. tricolor* in central Peru at 2,500 m, where their elevational ranges abut. Of the eight localities north of the Marañón, six involve *A.*

schistaceus with either *A. pallidinucha* or *A. leucopsis*.

Venezuelan Andes.—In the Venezuelan Andes, the pattern of elevational distribution does not differ substantially between the eastern and western slopes, and so the two were combined into one diagram (Fig. 4). Two species, *A. schistaceus* and *A. semirufus*, are found throughout, the former above 2,000 m and the latter below 2,100 m. *Atlapetes pallidinucha* is known from four localities at upper elevations in the Eastern Andes in western dept. Táchira. *Atlapetes albofrenatus* is found at a wide range of elevations in dept. Mérida, where it appears to interrupt the latitudinal distribution of *A. semirufus*. At only three (3.9%) of 77 localities has more than one species been found.

Santa Marta Mountains.—In the Santa Marta Mountains, only one species, *A. melanocephalus*,

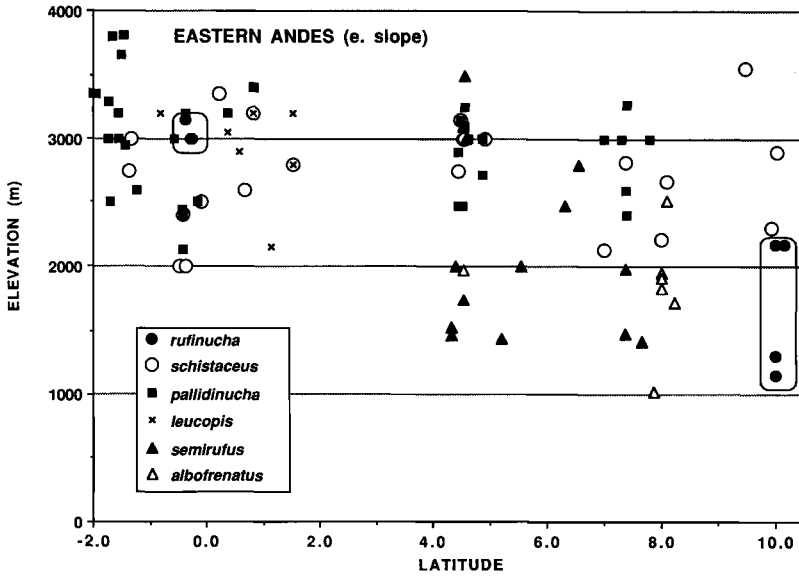


Fig. 3. Distribution of six species of *Atlapetes* on eastern slope of Eastern Andes from central Ecuador to northern Colombia. Each point represents locality from which one or more specimens of species obtained. Boxes enclose areas where *A. rufinucha* found. Included are a few localities in humid forest at Cordillera Colán on western (not eastern) slope of extreme northern tip of Eastern Andes in dept. Amazonas, northern Peru. Absence of specimens of any species in Colombia from about 1°45' in dept. Caquetá to 4° in dept. Meta (ca. 300 km) apparently indicates major gap in collecting efforts, one of largest in Andes. Same gap appears in distribution of Andean cracids mapped by Remsen and Cardiff (1990).

is found (Fig. 5). As is typical where only one species is found, *A. melanocephalus* occurs from the lower limit of cloud forest to timberline.

Eastern Andes of Colombia (western slope).—Six

species are found on the western slope of the Eastern Andes of Colombia (Fig. 6). *Atlapetes rufinucha* is known from five midelevation localities from about 5°45' to 6°30'N and also from

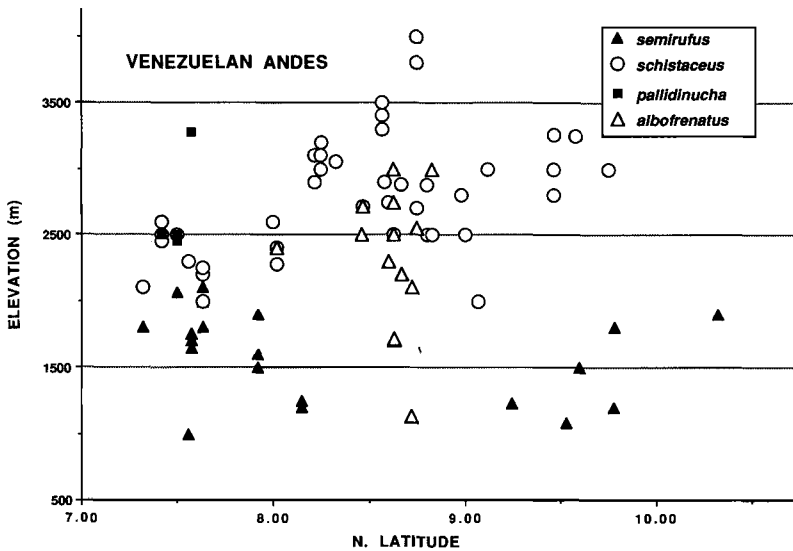


Fig. 4. Distribution of four species of *Atlapetes* in Andes of Venezuela; each point represents locality from which one or more specimens of species obtained.

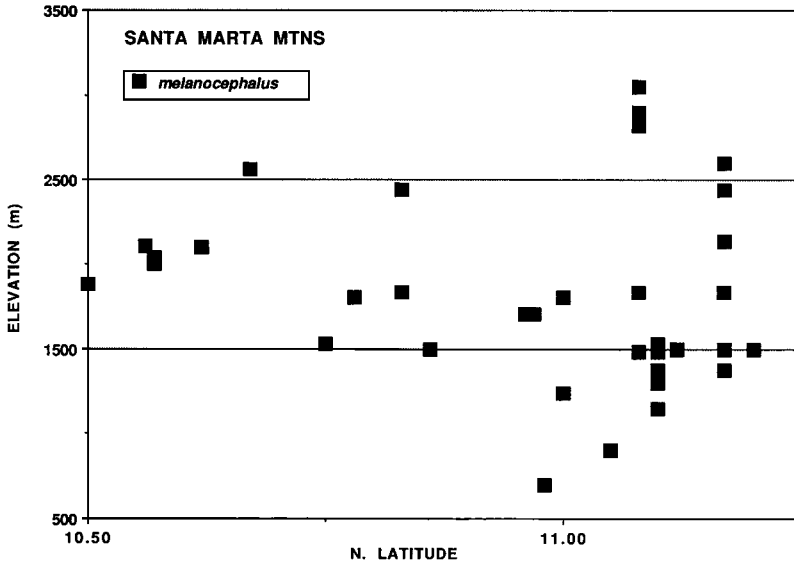


Fig. 5. Distribution of *Atlapetes melanocephalus* in Santa Marta Mountains of Colombia, where this is only species of *Atlapetes* found; each point represents locality from which one or more specimens of species obtained.

elevations below 1,700 m on the western slopes of the Perijá Mountains; no other species of *Atlapetes* has been collected at these localities. *Atlapetes schistaceus* replaces *A. rufinucha* above 1,700 m in the Perijá Mountains and is found above 2,500 m elsewhere, where it seems to

overlap heavily with *A. pallidinucha*. *Atlapetes gutturalis* is found only below about 2,000 m and primarily south of 5°N. Overlap in general distribution among the other species appears to be high, although at 126 (93.3%) of 135 localities, only a single species has been collected. At two

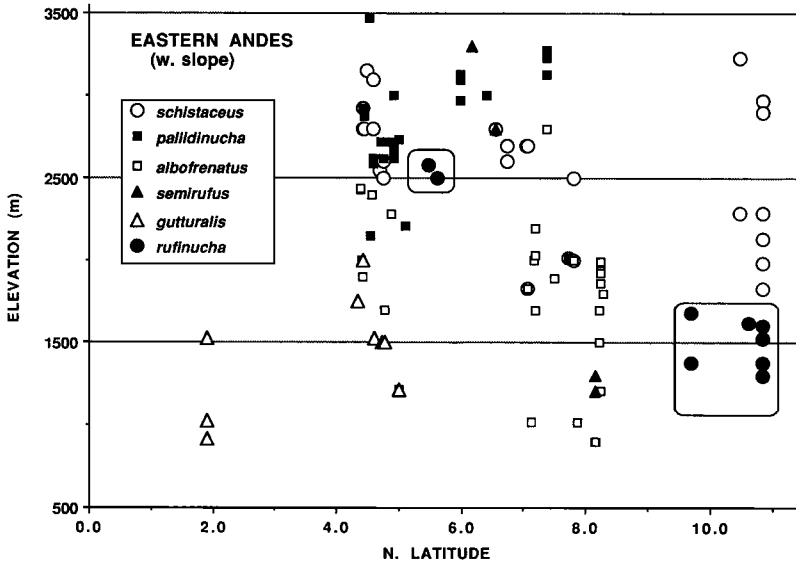


Fig. 6. Distribution of six species of *Atlapetes* on western slope of Eastern Andes of Colombia. Each point represents locality from which one or more specimens of species obtained. Boxes enclose areas where *A. rufinucha* found. Absence of high-elevation localities at southern end of range and again between 8° and 10°N reflects low elevations of Andes in those regions. Absence of specimens of any species in dept. Huila from about 2°N to about 4°N (ca. 250 km) apparently indicates major gap in collecting efforts.

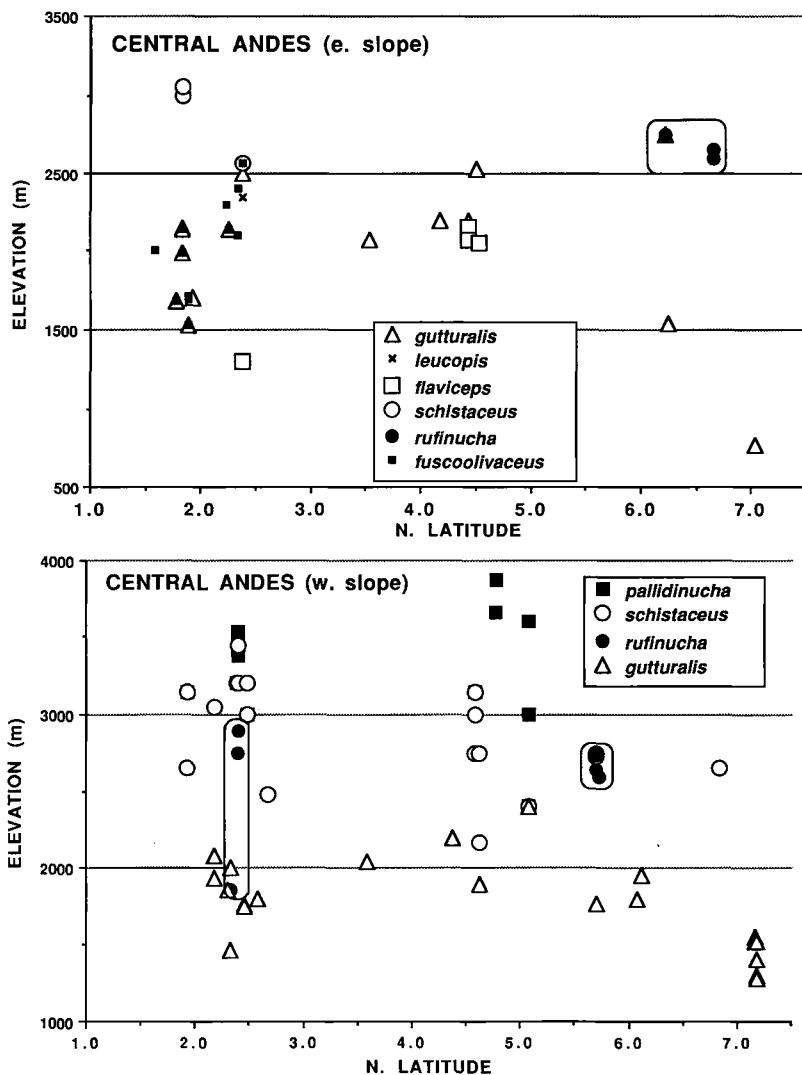


Fig. 7. Distribution of six species of *Atlapetes* on eastern and western slopes of Central Andes of Colombia. Each point represents locality from which one or more specimens of species obtained. Box encloses limits of *A. rufinucha* distribution. On western slope, localities at northern end of range where *A. rufinucha* is known represent subspecies *elaeoprurus*, whereas those at southern end of range represent *A. r. cauae* (Paynter 1978).

of the other nine localities, more than two species have been collected (Appendix).

Central Andes of Colombia.—On the eastern slope of the Central Andes in Colombia, *A. rufinucha* is known from only four localities at upper elevations at the northern end of the range (Fig. 7). *Atlapetes schistaceus* is known from only three localities at upper elevations at the southern end of the range. Otherwise, patterns of segregation are not clear. More than one species has been collected at 5 (13.2%) of 38 local-

ities in the region; all five involve *A. gutturalis* with either *A. fuscoolivaceus* or *A. flaviceps* (Appendix). The record of *A. flaviceps* at the southern end of the range pertains to the birds photographed by J. S. Dunning near La Plata Vieja, dept. Huila (in Dunning 1982); although *flaviceps* and *fuscoolivaceus* may replace each other at different elevations where their distributions come together (Ridgely and Gaulin 1980), overall they seem to be latitudinal replacements, not elevational replacements as suggested by Hilty

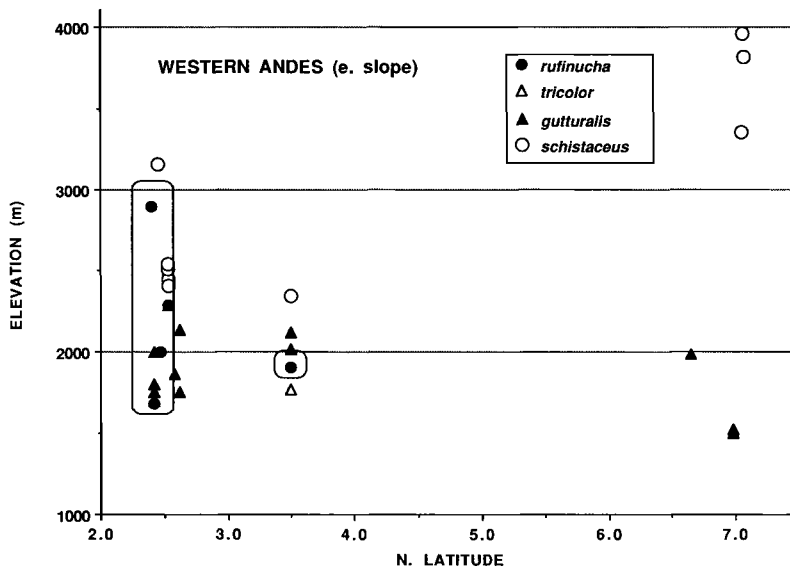


Fig. 8. Distribution of four species of *Atlapetes* on eastern slope of Western Andes of Colombia. Each point represents locality from which one or more specimens of species obtained. Boxes enclose limits of distribution of *A. rufinucha*. *Atlapetes tricolor* known from only single old specimen from San Antonio, the type locality for the species; however, Paynter (1978) and Hilty and Brown (1986) questioned authenticity of this record. Because summit Andes at this latitude is relatively low, perhaps record represents a wanderer from western slope. Absence of specimens of any species from about 3°30'N in northern dept. Valle to about 6°30'N in central dept. Antioquia (ca. 300 km) apparently indicates major gap in collecting efforts, one of largest in Andes.

and Brown (1986). Although Meyer de Schauensee (1964), Paynter (1978), and Hilty and Brown (1986) stated that *A. pallidinucha* occurs throughout Central Andes, and Ridgely and Tudor (1989) listed it only for eastern slope of Central Andes, we cannot find any specific specimen records for the eastern slope.

On the western slope of the Central Andes of Colombia, *A. pallidinucha* is found mainly at high-elevation localities, and *A. gutturalis* is typically the only species found below 2,100 m (Fig. 7). At intermediate and upper elevations, *A. schistaceus* is found throughout. *Atlapetes rufinucha* has been found at two, widely separated regions. More than one species has been collected at 5 (8.9%) of 56 localities. Four of the five involve *A. pallidinucha* with *A. schistaceus* at upper elevations; the fifth is the only locality in the Andes where both *A. rufinucha* and *A. schistaceus* have been collected.

Western Andes.—On the eastern slope of the Western Andes of Colombia, *A. rufinucha* is known from six localities at the southern end of the range and appears to overlap in elevational and latitudinal distribution with the other three species (Fig. 8). *Atlapetes schistaceus* is

known only from upper elevations; the gap in its distribution may be due in part to absence of high elevations in much of the Western Andes (Chapman 1917). More than one species has been collected at three (10.3%) of 29 localities, all involving *A. gutturalis* with either *A. rufinucha* or *A. schistaceus*.

On the western slope of the Western Andes from Colombia to northern Peru, elevational and latitudinal separation among the five species there is relatively clear (Fig. 9). From about 2°30'N in Colombia to about 3°S in southern Ecuador, *A. rufinucha* is found primarily above 2,000 m. South of this point, its elevational distribution expands downwards to near the lower limit of humid cloud forest apparently in response to the absence of *A. tricolor*, which occupies lower elevations from about 3°30'N to 3°30'S. *Atlapetes gutturalis* appears to replace *A. tricolor* at northern latitudes. *Atlapetes schistaceus* is known only from two high-elevation localities at the northern end of the range and one near the Equator. At none of 113 localities has more than one species been collected. We did not include several species of gray-and-white *Atlapetes* known from the western slope of the

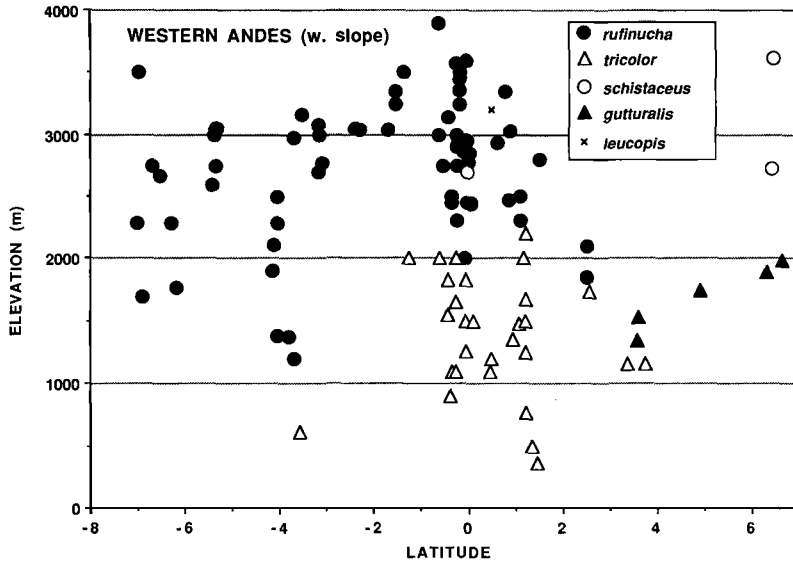


Fig. 9. Distribution of five species of *Atlapetes* on western slope of Western Andes from Colombia to northern Peru; each point represents locality from which one or more specimens of species obtained. Absence of high-elevation localities from about 2° to 6°N in Colombia reflects low elevation of summit of Western Andes.

Western Andes found from southern Ecuador to southern Peru because these species do not occur in cloud forest but in the dry woodland and scrub characteristic of lower elevations of the Andes at these latitudes (Paynter 1972, Fjeldså and Krabbe 1990). Presumably, these species would fill in the gaps in *Atlapetes* distribution at lower elevations at the southern end of the range.

When we pooled data from all regions, more than one species was found at 35 (4.0%) of 869 localities mapped (excluding Santa Marta Mountains, where only one species occurs). The unequal distributions of the various species, combined with the unequal opportunities for overlap in species-rich versus depauperate areas, complicate statistical analyses of any deviation from chance of the distribution of species' overlaps. However, one trend is noteworthy. Of these 35 localities (Appendix), 27 (77%) involved overlap between a member of Paynter's *albinucha* species group (*pallidinucha* or *gutturalis*) with a member of the *pileatus* or *schistaceus* groups, whereas only 8 (23%) involved overlap between members of either the *pileatus* or *schistaceus* groups. Although either *A. pallidinucha* or *A. gutturalis* were collected at only 179 (31.9%) of the 561 localities within their geographic ranges, they were involved in a

much higher proportion of the multispecies localities there (27 of 33; 81.8%) than expected by chance ($X^2 = 33$, $P < 0.001$; Table 1).

DISCUSSION

For many regions of the Andes, only one species of *Atlapetes* occupies any given elevational area. The gaps in the distribution of *A. rufinucha* are for the most part filled neatly by one or more other species of *Atlapetes*. Also, at latitudes where only one species, including *rufinucha*, occurs, that species tends to occupy the entire elevational gradient, whereas in areas with more than one species, elevational ranges are more constricted. For example, in the three areas where *rufinucha* is the only *Atlapetes*, the range of elevations occupied spans 1,700 m (e. slope E. Andes in n. Peru south of the Marañón), 2,400 m (w. slope W. Andes in s. Ecuador), and 3,150 m (e. slope E. Andes in s. Peru and n. Bolivia). In contrast, in 10 areas where *rufinucha* overlaps with other *Atlapetes* species, the mean elevational range is only 750 m (range 100–2,100 m). Similar patterns have been found for other Andean birds (Terborgh and Weske 1975, Remsén and Cardiff 1990) and birds of montane New Guinea (Diamond 1973). These patterns and results from "natural experiments" are consistent

TABLE 1. Synopsis of 906 specimen locality records of 14 species of *Atlapetes* from humid Andes. Diagonal cells contain total number of locality records in data base. Single numbers to left of diagonal indicate number of specimen localities where the two species have been collected. Dashes indicate pairs that do not overlap latitudinally anywhere in same mountain range. Double numbers to right of diagonal indicate number of occurrences of row species within latitudinal range of column species, followed by number of occurrences of column species within latitudinal range of row species.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 <i>albofrenatus</i>	60	0/0	0/0	0/0	0/0	13/8	0/0	0/0	0/0	29/36	2/5	50/53	16/6	0/0
2 <i>citrinellus</i>	—	24	0/0	6/6	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0
3 <i>flaviceps</i>	—	—	4	0/0	0/0	4/6	1/1	0/0	0/0	0/0	0/0	0/0	0/0	0/0
4 <i>fulviceps</i>	—	0	—	41	0/0	0/0	0/0	0/0	0/0	0/0	13/48	0/0	0/0	0/0
5 <i>fuscoolivaceus</i>	—	—	0	—	13	12/13	0/0	0/0	0/0	0/0	0/0	11/3	0/0	0/0
6 <i>gutturialis</i>	3	—	1	—	4	72	1/1	0/0	0/0	22/41	23/17	52/75	0/0	3/3
7 <i>leucopis</i>	—	—	0	—	0	0	10	0/0	0/0	8/25	1/0	9/13	0/0	1/1
8 <i>leucopterus</i>	—	—	—	—	—	—	—	2	0/0	2/0	2/0	0/0	0/0	0/0
9 <i>melanocephalus</i>	—	—	—	—	—	—	—	—	37	0/0	0/0	0/0	0/0	0/0
10 <i>pallidinucha</i>	3	—	—	—	—	2	0	0	—	107	18/33	98/91	34/29	0/0
11 <i>rufinucha</i>	0	—	—	0	—	1	0	0	—	2	243	38/34	0/0	32/17
12 <i>schistaceus</i>	5	—	0	—	—	4	2	—	—	14	1	185	33/43	34/57
13 <i>semirufus</i>	0	—	—	—	—	0	—	—	—	0	0	0	45	0/0
14 <i>tricolor</i>	—	—	—	—	—	—	—	—	—	—	0	2	—	63

with predictions of the interspecific-competition hypothesis (Diamond 1973, Terborgh and Weske 1975) and are not predicted by autecological hypotheses, such as that of Graves (1988: 50). Such natural experiments, however, are always vulnerable to criticism because they require the "all-else-being-equal" assumption (Wiens 1989). We use the relative constancy of elevational distributions of most other Andean bird species (Graves 1985, Remsen and Cardiff 1990), many of which are more highly specialized in their use of habitat and foraging substrates than are *Atlapetes* species, as circumstantial evidence in support of this assumption; the distributions of most other species imply that they do find these areas equivalent.

The areas where more than one species of *Atlapetes* overlap in elevational distribution are primarily the eastern slope of the Eastern Andes in Ecuador and Colombia, the Central Andes of Colombia, and the eastern slope of the Western Andes of Colombia. These are also the regions of maximum species richness in the genus, with as many as six species found on the eastern slope of the Central Andes and either slope of the Eastern Andes of Colombia. Virtually all specimen records from these regions were obtained from the first 40 years of this century, when a lack of good maps may have affected accuracy of elevations for localities and when some collectors frequently roamed up- and down-slope from a locality yet labeled all specimens as if from the same locality. Therefore,

we wonder what proportion of the substantial overlaps indicated in our diagrams are artifacts of poor resolution of the data. Our mapping technique is probably inadequate for distinguishing between syntopy and fine differences in elevation and habitat. F. G. Stiles (in litt.) has found that, at many localities in Colombia, at least two *Atlapetes* species may be truly syntopic, but that at these localities, the species differed in habitat or microhabitat use.

Anecdotal information on natural history of brush-finches in Paynter (1978), Hilty and Brown (1986), Ridgely and Tudor (1989), and Fjelds  and Krabbe (1990) does not reveal any consistent, major habitat or microhabitat differences among the species analyzed; most are described as fairly common to common at the edge of humid forest and foraging mainly in the first 5 m above ground. The following suggestions of ecological differences among species were noted. Ridgely and Tudor (1989) considered *A. leucopis* to be more like *Buarremon* brush-finches in being reclusive and evidently more terrestrial; this species is also notably larger than the others (Paynter 1978). Ridgely and Tudor (1989) reported that *A. gutturalis* was more tolerant of deforested conditions than other *Atlapetes*. Paynter (1978), Hilty and Brown (1986), Ridgely and Tudor (1989), and Fjelds  and Krabbe (1990) noted that *A. albofrenatus* is found in dry woodland and scrub in some areas (but this observation may come from a single anecdotal observation reported to Paynter). Hilty and Brown

(1986), Ridgely and Tudor (1989), and Fjeldså and Krabbe (1990) noted that *A. rufinucha* and *A. schistaceus* tended to be more arboreal than other *Atlapetes*; Remsen's (1985) data on foraging heights of *A. rufinucha* indicate that the mean height above ground was nearly 5 m, but comparable data for other species are not available. Finally, our finding that members of Paynter's *pileatus* species-group overlap with members of other species groups much more frequently than expected by chance hints that there might be ecological differences between *A. pallidinucha* or *A. gutturalis* versus other *Atlapetes* species. F. G. Stiles' (in litt.) recent experience in Colombia has confirmed that such ecological differences exist, with *pallidinucha*, *gutturalis*, *tricolor*, and *albofrenatus* typically occurring in more open, scrubby or drier areas than other species where they overlap with other *Atlapetes* species.

Regardless of the degree of true overlap among brush-finches, in general the initial question of why the distribution of *A. rufinucha* is so patchy appears to be related to the distribution of *A. schistaceus* and, to a lesser extent, as noted by Paynter (1978), that of *A. tricolor*. The near-perfect complementarity of their distributions is striking. Although at least one of these three species has been collected at 453 (60.1%) of the 754 Andean specimen localities in our data base, at only 3 (0.7%) of these 453 localities have two of these species been collected. This pattern can be interpreted as circumstantial evidence that interspecific competition influences distributions, because "natural experiments" reveal that *rufinucha* occupies a broader range of elevations where *schistaceus* is absent.

If interspecific competition controls the distribution of these species, then reconstruction of the history of this pattern becomes complex. The problem is, how can one species occur on either side of the latitudinal distribution of another to produce such a checkerboard pattern? As discussed by Remsen and Cardiff (1990) for guans, it is unlikely that the disjunct patterns exhibited by all three *Atlapetes* species are the result of long-distance dispersal. All have short, rounded wings that suggest that long-distance movements are unlikely, and there are no extralimital records for any species other than perhaps some limited elevational wandering. Therefore, it also seems unlikely that these brush-finches could cross hundreds of kilometers of unsuitable habitat, either high-ele-

vation puna or low-elevation tropical forest, to bypass the latitudinal distribution of another species to colonize areas beyond the distribution of the other species. Paynter (1978) proposed that pulses of latitudinal dispersal within suitable habitat by one or more species followed by climatic changes would produce temporary regions of broad overlap followed by extinction of one or more species within a given latitudinal region (as demarcated by barriers such as dry river canyons). Graves (1988) outlined why the linearity of the ranges of Andean birds makes them especially susceptible to local extinctions, thereby creating patchy distributions such as that of *A. rufinucha*. T. A. Parker (pers. comm.) and G. Graves (pers. comm.) suspect that the range limits and population sizes of many Andean *Atlapetes* have expanded in historic times because destruction of closed-canopy forest has created more suitable habitat. We find a combination of these proposals to be the most reasonable mechanism for creation of the mosaic distributions in *Atlapetes*. Furthermore, in those latitudinal regions where more than one species occurs, the current distribution pattern of elevational separation may not be at equilibrium, as noted by Remsen and Cardiff (1990) for the current distribution pattern of Andean cracids. Unfortunately, no data are available to determine whether range boundaries have shifted in historic times.

We introduce a novel hypothesis that would remove the need for such complex historical zoogeography to explain the current pattern. This hypothesis abandons current species limits and proposes that the names "*rufinucha*," "*schistaceus*," and perhaps "*tricolor*" refer only to recurring color patterns within a single lineage that do not unite sister taxa. In other words, the three color patterns are all part of a single widespread lineage, with adjacent populations, regardless of color, each other's closest relative. With no evidence for any degree of interbreeding between any sympatric or parapatric populations of different color groups, delimitation of biological species would be complex.

Although Paynter (1978) placed *rufinucha* and *schistaceus* in different lineages within the genus, these two forms are extremely similar to each other except in the presence of yellow pigment. Many subspecies of *rufinucha* and *schistaceus* are virtually indistinguishable in black-and-white photographs, and I can find no phenotypic character other than "yellow vs. gray"

that distinguishes *rufinucha* from *schistaceus*. Furthermore, the subspecies of *rufinucha* that have a conspicuous white wing speculum (*elaeoprorus*, *caucae*, and *latinuchus*) are geographically adjacent to the only population of *schistaceus* (*A. s. schistaceus*) that shares this plumage character. Similarly, the only subspecies of *rufinucha* with the throat and underparts conspicuously clouded with dark gray color (*A. r. melanolaemus*) is geographically adjacent to the population of *schistaceus* that also has the darkest gray underparts (*A. s. canigenis*). Finally, adjacent populations of *rufinucha* and *schistaceus* in Peru and Bolivia are more similar morphometrically to one another than they are to other populations of their same "species" elsewhere (D. Ruhl unpubl. data), although this is not the case in Colombia (G. R. Graves in litt). Until the true phylogeny of these taxa is known, we cannot determine whether these observations represent coincidences, examples of convergent evolution, or evidence of sister relationships between adjacent taxa. An analysis of vocal differences among currently recognized taxa would probably provide the simplest test of these hypotheses.

If *rufinucha* and *schistaceus* were simply yellow and gray representatives, respectively, of the same lineage, then the alternating pattern of yellow and gray populations along the Andes would provide yet another example of the "leap-frog" pattern of geographic variation so prevalent in lineages of Andean birds (Remsen 1984): retention of primitive plumage characters leaves peripheral populations more similar phenotypically to each other than they are to populations with derived characters that separate them geographically. Yellow and gray are the colors involved in three of the 25 lineages that show the leap-frog pattern (*Hemispingus superciliaris*, *Basileuterus coronatus*, and *Chlorospingus ophthalmicus*).

The difference between yellow and gray plumage is dramatic to the human eye. This difference certainly influenced Paynter's (1978) designation of lineages within *Atlapetes*; his *schistaceus* group consists of all species with gray plumage (Paynter 1972). However, the genetic difference between yellow and gray might be negligible. Johnson and Brush (1972) and Brush and Johnson (1976) showed that the difference between yellow and gray pigments in some passerines is simply a difference in concentration of lutein in the feathers and that extraction of

lutein from an olive-yellow feather produces a gray one. The genetic and chemical bases of yellow and gray plumage in *Atlapetes* is not known.

If *rufinucha* and *schistaceus* are not alternating gray and yellow representatives of the same lineage, then yellow or gray plumage is a character that defines the two separate lineages. If so, we propose that *rufinucha* and *schistaceus* are sister taxa, not distant relatives as proposed by Paynter (1978). This cluster of taxa also may include *A. fuscolivaceus* and *A. flaviceps*, which Paynter (1978) proposed were sister taxa of *A. tricolor*, a species he proposed was closely related to *rufinucha*; Paynter also pointed out that these two taxa fill a latitudinal gap in the range of *A. rufinucha*.

We wonder how many other examples might exist in which current taxonomy has overemphasized the importance of plumage coloration, particularly yellow versus gray. For example, such overemphasis obscured the true relationship between *Chlorospingus pileatus* and *C. "zeledoni"* for more than 65 years until Johnson and Brush (1972) showed that "*zeledoni*" was just a local, gray color morph of *pileatus*. Lowery and Monroe (1968) evidently placed too much importance on the difference between yellow and gray plumage when they placed two sister species of *Basileuterus* wood-warblers (*B. culicivorus* and *B. hypoleucus*) in separate sections of the genus (Remsen and Traylor 1989:55). Within *Atlapetes*, in addition to the *rufinucha-schistaceus* example, the predominantly gray *A. rufigenis* and the predominantly yellow *A. fulviceps*, currently placed in separate lineages by Paynter (1978), also are probable sister taxa (as suggested to us by G. F. Barrowclough; see also Fjelds  1992:61). Also, *A. albofrenatus* looks like a yellow-green version of some subspecies of *A. schistaceus*, as much or more so than does *A. rufinucha*, although Paynter (1978) also placed *A. albofrenatus* in a different lineage than *A. schistaceus*. (Paynter pointed out, however, that *A. albofrenatus* was very similar to *A. rufinucha* and that they seemed to replace each other in the Eastern Andes.) In contrast, Paynter placed *A. pileatus* in the same lineage as *rufinucha* and other yellow *Atlapetes* because of their shared yellow plumage and rusty crowns; however, unique features (pale tarsi, absence of malar stripe) and geographic distribution (endemic to Mexico) suggest that *A. pileatus* is the most divergent species within the genus and that its

similarity to the *rufinucha* group, no member of which occurs north of Colombia, is only superficial. This prediction is confirmed by Hackett's (1992) genetic analysis of a subset of *Atlapetes* species, which placed *A. pileatus* as the basal branch within the genus (excluding *Buarremon*).

Many sister taxa differ only or primarily in being yellow or gray. Within *Atlapetes*, for example, *A. albinucha* and *A. gutturalis* differ only in this way. A familiar North American example is the Nashville Warbler (*Vermivora ruficapilla*) and Virginia's Warbler (*V. virginiae*; Brush and Johnson 1976, Johnson 1976). The Black-throated Gray Warbler (*Dendroica nigrescens*) and Townsend's Warbler (*D. townsendi*) are virtually identical in pattern and differ primarily in amount of yellow, presumably a matter of lutein concentration; Bermingham et al. (1992) showed that Black-throated Gray Warbler is the sister taxon to a cluster of yellow-green species that includes Townsend's Warbler. Bird groups rich in yellow and gray species, such as Tyrannidae, Vireonidae, Zosteropidae, and Parulinae, may have several such sister taxa relationships.

Johnson and Brush (1972) noted that a difference in pigment concentration, which may generate conspicuous phenotypic differences, is perhaps the simplest mechanism for color divergence among closely related bird taxa. Whether this mechanism has been responsible for a complex series of changes in plumage within a single lineage, or whether yellow and gray do indeed define lineages in *Atlapetes*, awaits a phylogeny based on genetic or non-plumage characters.

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APPENDIX. Localities where more than one *Atlapetes* species collected. Headings correspond to regions featured in Figures 2-9. Elevations converted to meters for localities with elevations on original labels in feet.

Eastern Andes (eastern slope)

Colombia: dept. Cundinamarca, San Miguel, 2,800 m (*pallidinucha, schistaceus*); dept. Cundinamarca, Repr. de Sisga, 2,500 m (*pallidinucha, schistaceus*); dept. Cundinamarca, Boquerón de Chipaque, 3,150 m (*pallidinucha, schistaceus*); dept. Nariño, Llorente, 3,200 m (*leucopis, schistaceus*).

Ecuador: prov. Napo, Cuyujúa, 2,400 m (*pallidinucha, schistaceus*); prov. Azuay, Palmas, ca. 2,500 m (*leucopis, schistaceus*).

Peru: dept. Cajamarca, Cerro de Chinguela, 2,898 m and 2,623 m (*pallidinucha, rufinucha*); dept. Pasco, Cumbre de Ollón, 2,500 m (*schistaceus, tricolor*); dept. Junín, Huacapistani, 2,500 m (*schistaceus, tricolor*).

Venezuelan Andes

Estado Mérida, Carbonera, 2,500 m (*albofrenatus, schistaceus*); estado Mérida, Los Nevados, 2,711 m (*albofrenatus, schistaceus*); estado Táchira, Cerro Las Copas, 2,500 m (*pallidinucha, schistaceus*).

Eastern Andes of Colombia (western slope)

Dept. Norte de Santander, Las Ventanas, 2,000 m (*albofrenatus, schistaceus*); dept. Santander, Hacienda Las Vegas, 1,830 m (*albofrenatus, pallidinucha, schistaceus*); dept. Cundinamarca, Aguabonita (Silvania), 2,300 m (*albofrenatus, pallidinucha*); dept. Cundinamarca, Chicó, 2,700 m (*pallidinucha, schistaceus*); dept. Cundinamarca, El Peñon, 2,928 m (*pallidinucha, schistaceus*); dept. Cundinamarca, La Aguadita, 2,300 m (*albofrenatus, gutturalis, pallidinucha, schistaceus*); dept. Cundinamarca, Laguna de Pedropalo, 2,010 m (*albofrenatus, gutturalis*); dept. Cundinamarca, La Vega, 1,215 m (*albofrenatus, gutturalis*); dept. Cundinamarca, Monserrate, 3,160 m (*pallidinucha, schistaceus*).

Central Andes of Colombia

Eastern slope: dept. Tolima, Río Toche, 2,074 m (*gutturalis, flaviceps*); dept. Huila, La Candela, 10 mi SW San Agustín, 1,983 and 2,135 m (*fuscoolivaceus, gutturalis*); dept. Huila, near San Agustín, 1,523 m (*fuscoolivaceus, gutturalis*); dept. Huila, La Palma, 1,678 m (*fuscoolivaceus, gutturalis*).

Western slope: dept. Antioquia, Páramo Sonsón, 2,745 m (*pallidinucha, schistaceus*); dept. Caldas, El Zancudo, 2,400 m (*gutturalis, pallidinucha, schistaceus*); dept. Cauca, La Guneta, 3,142 m (*pallidinucha, schistaceus*); dept. Cauca, Almaguer, 3,142 m (*pallidinucha, schistaceus*); dept. Cauca, Puracé, Km 10-11, 3,447 m (*rufinucha, schistaceus*).

Western Andes (western slope)

Dept. Cauca, Cerro Munchiquito, 2,288 m (*gutturalis, rufinucha*); dept. Cauca, Cerro Munchique, 2,509 and 2,539 m (*gutturalis, schistaceus*).
