

## DISTRIBUTION PATTERNS OF BUARREMON BRUSH-FINCHES (EMBERIZINAE) AND INTERSPECIFIC COMPETITION IN ANDEAN BIRDS

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**ABSTRACT.**—Two species of Andean brush-finches, *Buarremon* (formerly *Atlapetes*) *torquatus* and *B. brunneinuchus*, show an interdigitating pattern of distribution in the Andes that we interpret as the result of competition between them. Plotting 590 specimen localities by latitude and elevation reveals that the two species have complementary, parapatric distributions with minimal overlap. More importantly, where only one species occurs, that species usually occupies the entire elevational range in that region. Furthermore, the usual relative position of the two species, with *B. torquatus* at high and *B. brunneinuchus* at low elevations, is reversed in two regions. These “natural experiments” suggest that elevational limits are unlikely to be governed in these two species by autecological factors and that interspecific competition is the process most likely to generate such a pattern. However, our re-evaluation of other data interpreted to support the prevalence of interspecific competition in determining elevational limits of other Andean birds suggests that its role has not been properly resolved. Received 28 June 1993, accepted 24 October 1993.

BIRD DISTRIBUTIONS in the Andes Mountains are characterized by vertical segregation and relatively uniform elevational ranges throughout the range of each species (Chapman 1917, 1926). One striking exception to this generalization is the elevational distribution of *Buarremon* (formerly *Atlapetes*; see below) *torquatus* (Stripe-headed Brush-Finch; Emberizinae), which in some areas occurs from near timberline to the lower limit of cloud forest, but in other areas has a narrow elevational distribution (Paynter 1978, Hilty and Brown 1986, Fjelds  and Krabbe 1990).

Paynter (1978) and Fjelds  and Krabbe (1990) proposed that the areas where *B. torquatus* occupied narrow elevational ranges corresponded to those areas where a congener, *B. brunneinuchus* (Chestnut-capped Brush-Finch), was present, suggesting that interspecific competition governed elevational limits in these two species. Their similarity in body size, shape, plumage, foraging behavior (mainly terrestrial), and habitat (undergrowth of humid montane forest) makes these brush-finches likely competitors. The purpose of our analysis was to evaluate this hypothesis by plotting precisely the latitudinal and elevational distributions of the two species,

and then comparing the distribution of *B. torquatus* in areas with and without *B. brunneinuchus*. The interspecific competition hypothesis predicts that the two distributions should be complementary, with perhaps minimal sympatry where ranges abut and, more importantly, that one species should expand its range of elevations where the other is absent. Other hypotheses, such as the autecological hypothesis or the historical-accident hypothesis (Remsen and Cardiff 1990), predict that the distributions of the two species should be independent of one another within the same habitat, climatological, or zoogeographic region, and that elevational limits of one species should not change where the other is missing.

Although Paynter (1978) previously mapped latitudinal distributions of *Buarremon* brush-finches from collecting localities, he was unable to analyze elevational distributions in a similar way because of the absence of elevational data from many collecting localities. However, with the recent completion of the gazetteers for all the Andean countries by Paynter and his colleagues (Paynter et al. 1975, Paynter and Traylor 1977, 1981, Paynter 1982, 1985, Stephens and Traylor 1983), mapping of elevational distributions is now feasible. Furthermore, 15 years of additional fieldwork since Paynter's analysis (1978) has generated much additional locality data, particularly in Peru and Bolivia. Absence of gazetteers for Middle America, where *B. brun-*

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*neinuchus* and *B. {torquatus} virenticeps* are widely sympatric, makes a similar analysis there much more difficult.

Because the taxonomy used herein differs from that in most current references, we offer the following explanations. Since Hellmayr (1938), all authors have treated *Buarremon* species as members of the genus *Atlapetes* (e.g. Parkes 1954, Meyer de Schauensee 1966, Paynter 1970, 1978, Ridgely and Tudor 1989, Fjelds  and Krabbe 1990, Sibley and Monroe 1990). However, Hackett (1992) recently found that *Buarremon* is not particularly closely related to *Atlapetes*. In fact, the only reason Hellmayr (1938) gave for the merger of *Buarremon* into *Atlapetes* was that the degree of "stoutness" of their bills showed no clear separation between the two groups. Subsequent authors have followed this merger without question, although bill size and shape are now recognized as characters highly subject to adaptive modification and often phylogenetically uninformative (e.g. Bock 1964). In contrast to species of *Atlapetes*, species of *Buarremon* are relatively secretive and forage almost exclusively on the ground (Ridgely and Tudor 1989, Fjelds  and Krabbe 1990). They do not share any plumage features that suggest to us a closer relationship to *Atlapetes* than to any other genus of medium-sized, towheelike emberizids of nongrassy habitats. However, their black-and-white plumage, breast band, and yellow area at the bend of the wing are strikingly similar to species in the genus *Arremon* (as reflected in derivation of generic name). Also, the dorsal plumage of *B. brunneinuchus* is virtually identical to that of the secretive, ground-foraging species of *Lysurus* of Costa Rica, Panama, and the Andes; Hackett (1992) found that genetic characters support a sister relationship between *Lysurus* and *Buarremon*. The dorsal plumage of *B. torquatus* is extremely similar to that of the ground-foraging *Pezopetes capitalis* of Costa Rica; Hackett (1992), however, found that genetic characters linked *Pezopetes* with *Atlapetes*, rather than *Buarremon*.

Controversy exists over species limits within the lineages in *Buarremon*. Some authors (e.g. Wetmore et al. 1984, Fjelds  and Krabbe 1990) have treated the black-headed, low-elevation taxa (*atricapillus* group) of southern Central America and northern Colombia, and occasionally (e.g. Paynter 1970) including Middle American *virenticeps*, as subspecies of *B. torquatus*. Most (e.g. Hellmayr 1938, Meyer de Schauensee 1966,

Paynter 1978, AOU 1983, Hilty and Brown 1986, Ridgely and Tudor 1989, Sibley and Monroe 1990), however, have treated them as separate species, although the Costa Rican taxon *costaricensis* has been variously assigned to *B. atricapillus* or to *B. virenticeps*. Paynter (1978) and Ridgely and Tudor (1989) considered the low-elevation *atricapillus* a separate species because they thought that it was parapatric, or nearly so, with high-elevation *B. torquatus*, with no sign of intergradation. As we show below, however, plotting of elevational distributions reveals that the two taxa are greatly separated in elevational distribution and that they are separated by intervening populations of *B. brunneinuchus*. Therefore, they have no opportunity to show any intergradation, the absence of which convinced Ridgely and Tudor (1989) to consider *atricapillus* a separate species. Furthermore, populations of *B. torquatus* occur at low elevations in many regions and, in fact, the four subspecies found in Venezuela (*perijanus*, *larensis*, *phaeopleurus*, and *phygas*) are restricted to low elevations. Therefore, the low-elevation distribution of *atricapillus* is not in itself evidence of a meaningful biological difference between it and the *torquatus* group. The great variability in plumage, particularly in the amount of black, in *B. torquatus* throughout the Andes (Chapman 1923) does not make the blacker head of *atricapillus* seem particularly different, and Paynter (1978) pointed out that character states showed a mosaic distribution among the *virenticeps*, *atricapillus*, and *torquatus* groups of subspecies. Although Hellmayr (1938) considered *atricapillus* a separate species, he was hesitant to do so, noting the close approach in coloration of *B. a. tacarcunae* (of extreme eastern Panama) to *B. t. assimilis* (the nearest Andean population of *torquatus* group). Wetmore et al. (1984:592) noted that the populations of eastern Panama, including *tacarcunae*, "form a nearly perfectly graded series between *costaricensis* of western Panama and Costa Rica, and *atricapillus* of South America. There can be no doubt that all belong to a single species." Ridgely and Tudor (1989) used this evidence to consider *costaricensis* a subspecies of *atricapillus*, although *costaricensis* is extremely similar phenotypically to typical members of the *torquatus* group, especially the closest taxon, *B. t. assimilis*. In contrast to Ridgely and Tudor (1989) and Sibley and Monroe (1990), we tentatively follow Wetmore et al. (1984) by treating all forms as subspecies of a single spe-

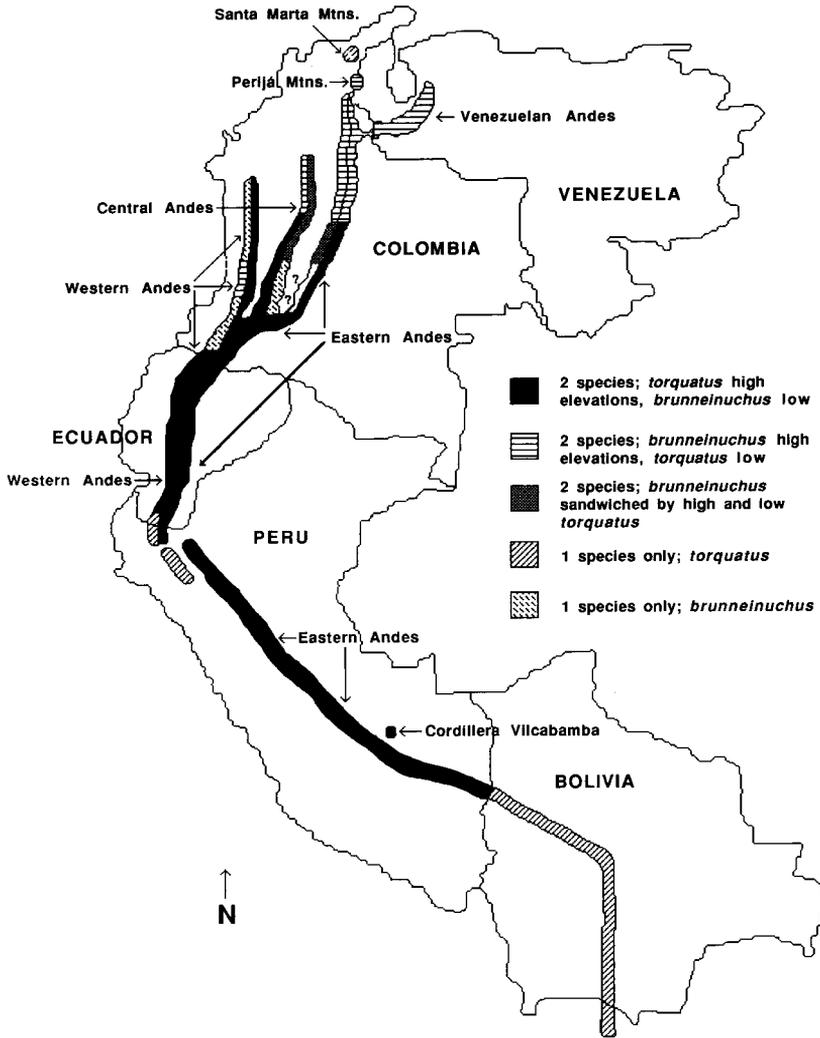


Fig. 1. Schematic representation of distribution of genus *Buarremon* in South America. Small sample sizes make interpretations of distributions tentative in many sections of Andes of Colombia.

cies. In the absence of nonanecdotal data on vocal differences, we consider the question of species limits to be unresolved. Nonetheless, no one has questioned that the *atricapillus* group and *torquatus* group are sister groups.

METHODS

We gathered specimen localities from major museums (see Acknowledgments) for both species of *Buarremon* on the humid slopes of the Andes Mountains from northern Venezuela and Colombia to northern Argentina. We analyzed the same regions (Fig. 1) as Remsen and Graves (1995), and also used their methodology for determining latitudes and elevations. Our final data base, those sites where one

or both species were collected and where both latitude and elevation were known, consisted of 586 localities, which represent the vast majority of all known localities for *Buarremon* in South America. See Remsen and Graves (1995) for a discussion of the difficulties and drawbacks of using data from specimen localities. Although species of *Buarremon* are more secretive than the species of *Atlapetes* studied by Remsen and Graves (1995), the near-ground foraging behavior of species of *Buarremon* make them even more prone to capture by mist nets than are *Atlapetes*.

RESULTS

In the Andes of Venezuela (Fig. 2), *B. torquatus* is known from low-elevation localities in two

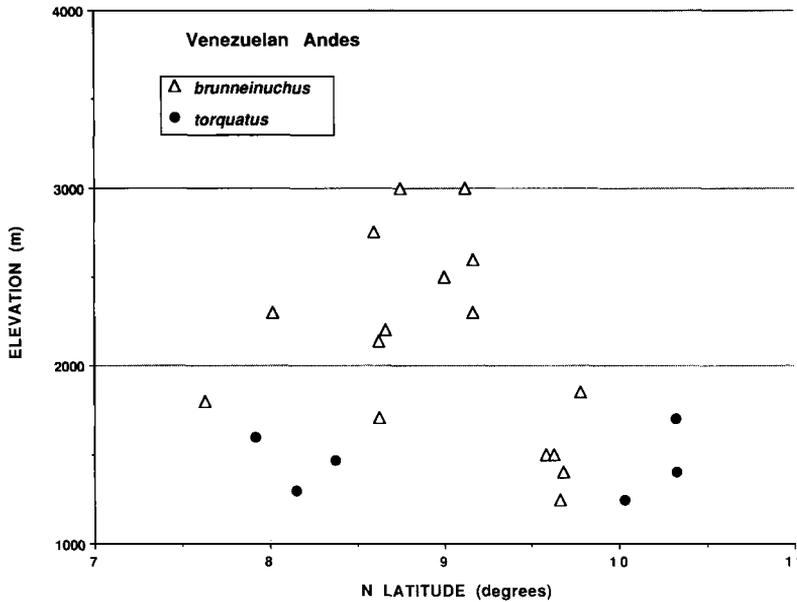


Fig. 2. Distribution of *Buarremon brunneinuchus* and *B. torquatus* in Andes of Venezuela; each point represents locality from which one or more specimens obtained. In this and other regions (represented in Figs. 2-7), lower limit of montane cloud forest usually is 1,200 to 1,300 m, and upper limit usually about 3,300 to 3,400 m. The two localities on left (south) actually are on eastern slope of main Eastern Andes, whereas those on right are in Cordillera de Mérida, which is isolated from main Andes (Vuilleumier 1971). The subspecies of *B. torquatus* is *B. t. larensis*, a member of *torquatus* group of subspecies.

areas, whereas *B. brunneinuchus* is found at higher elevations and is more widely distributed. However, *B. brunneinuchus* is found at low elevations in southern estado Lara, an area where *B. torquatus* has not been recorded. The two species have not been collected at the same locality.

In the isolated Santa Marta Mountains of northern Colombia (points north of about 10°45'N in Fig. 3), only *B. torquatus* is found, and it occupies the entire range of elevations with humid montane forest. In the Perijá Mountains of extreme northern Colombia and northwestern Venezuela (from 9°57' to 10°20'N in Fig 3) and also in the Eastern Andes of northern Colombia north of about 7°N, *B. brunneinuchus* is found mostly above 1,800 m, and *B. torquatus* is found mainly below 1,800 m, where the subspecies present is *B. t. perijanus*, a member of the *torquatus* group of subspecies (Paynter 1978), rather than the expected *atricapillus* group.

At about 5°N (dept. Boyacá, Colombia), however, the two species switch their relative elevational positions, with *B. torquatus* found mainly above 2,300 m and *B. brunneinuchus* mainly below 2,500 m. This situation remains unchanged to at least 14°S at the Peru-Bolivia bor-

der. Over this range of roughly 2,800 km, the boundary between *B. torquatus* and *B. brunneinuchus* fluctuates from 2,100 to 2,700 m, but their relative positions stay the same at any given latitude. South of 14°S, *B. brunneinuchus* drops out, and *B. torquatus* then dramatically expands its elevational distribution downward to include all elevations below 2,600 m usually occupied by *B. brunneinuchus*. South of about 18°S, in southern Bolivia and northern Argentina, *B. torquatus* disappears from elevations above 2,500 m, evidently because suitable habitat is scarce or absent. Throughout the eastern slope of the Eastern Andes, the two species have been collected at the same locality at only 4 (1.3%) of 314 localities (Palo Gordo, dept. Norte de Santander, Colombia; 33 road km NE Ingenio, dept. Amazonas, Peru; Playa Pampa, dept. Pasco, Peru; and Abra de Maruncunca, dept. Puno, Peru).

On the western slope of the Eastern Andes of Colombia (Fig. 4), the pattern is similar to that on the eastern slope in Colombia. The high-elevation species is generally *B. brunneinuchus* and the low-elevation species is *B. torquatus* (either *B. t. perijanus* or *B. t. atricapillus*). However, at about 4°N (dept. Huila), a high-elevation *B.*

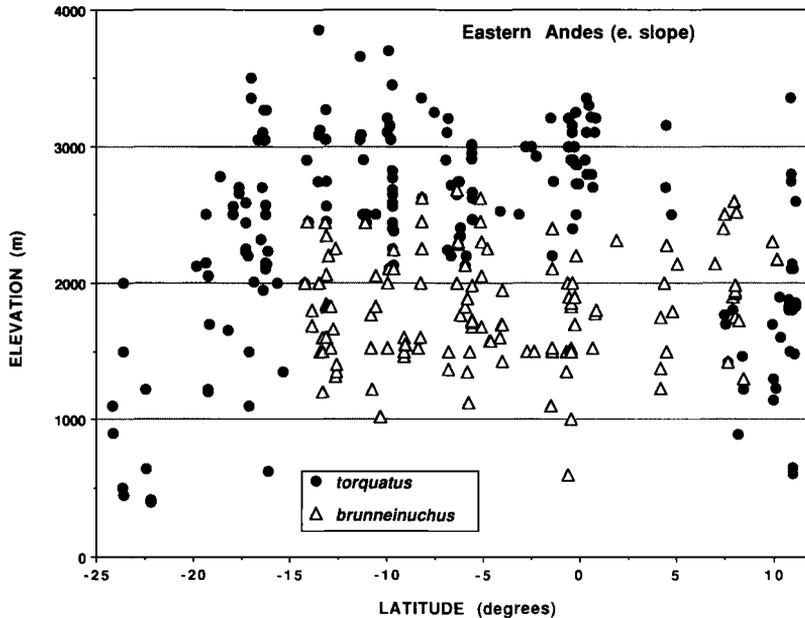


Fig. 3. Distribution of *Buarremon brunneinuchus* and *B. torquatus* on eastern slope of Eastern Andes from northern Argentina to northern Colombia, and also in Santa Marta Mountains of northern Colombia (all points north of ca. 10°45'N). Each point represents locality from which one or more specimens obtained. "Negative" latitudes are those south of Equator. Except for one record of *B. brunneinuchus*, neither species has been collected from about 4°N (dept. Cundinamarca, Colombia) to about 1°N (Colombia-Ecuador border). This 400-km hiatus reflects major gap in efforts to collect Andean birds. The same gap exists for Andean cracids (Remsen and Cardiff 1990), *Atlapetes* brush-finches (Remsen and Graves 1995), and to some extent in map of Colombian collecting localities in Paynter and Traylor (1981:282). Included in our map are a few localities in humid forest at Cordillera Colán on western slope at extreme northern tip of Eastern Andes in dept. Amazonas, northern Peru. Not plotted are data from Cordillera Vilcabamba, an isolated spur of eastern Andes in southern Peru, where *B. brunneinuchus* was recorded from 1,320 to 2,250 m, and *B. torquatus* from 2,640 to 2,830 m (Weske 1972).

*torquatus* population "sandwiches" *B. brunneinuchus* between high- and low-elevation populations of *B. torquatus*. Thus, the low-elevation form (*B. t. atricapillus*) is separated from the high-elevation form (*B. t. assimilis*) by about 1,500 m of elevation. South of 4°N, so few localities have been sampled that no pattern can be discerned. Two species have been collected at the same locality in this region at only 2 (4.3%) of 46 sites, both in the Perijá Mountains of Colombia (Monte Elías and Hiroca).

On the eastern slope of the Central Andes of Colombia (Fig. 5, upper panel), *B. brunneinuchus* occupies elevations from about 1,400 to 2,600 m. As on the western slope of the Eastern Andes, *B. brunneinuchus* appears to be "sandwiched" above and below by populations of *B. torquatus*, at least at northern latitudes (*B. t. atricapillus* at low elevations and *B. t. assimilis* at high elevations). Although locality records are

few, the two populations of *B. torquatus* so far have not been collected within 1,200 m elevation of one another. South of about 4°45'N, *B. torquatus* has not been collected, but apparently the appropriate elevations have not been sampled. Therefore, we cannot tell whether only *B. brunneinuchus* occurs there and occupies all elevations, or both species occur, with *B. brunneinuchus* occupying middle elevations only. Two species have been collected at the same locality at only 1 (4.6%) of 22 sites (La Sofia, dept. Caldas).

On the western slope of the Central Andes of Colombia (Fig. 5, lower panel), the localities where *B. brunneinuchus* has been collected are all at middle elevations and are bracketed above and below by populations of *B. torquatus*, again *B. t. atricapillus* at low elevations and *B. t. assimilis* at high elevations, separated by about 800 m of elevation. In contrast to the eastern slope, *B.*

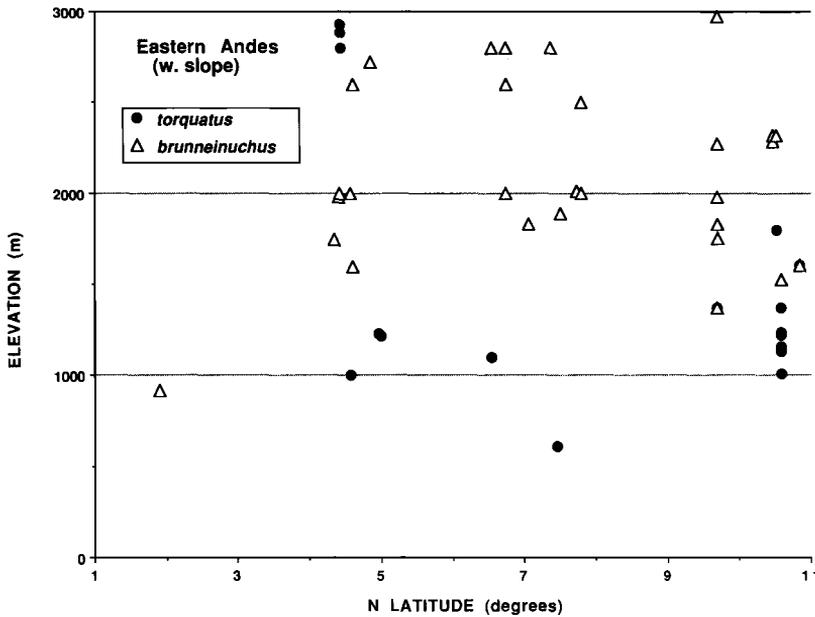


Fig. 4. Distribution of species of *Buarremon* on western slope of Eastern Andes of Colombia; each point represents locality from which one or more specimens obtained. Absence of high-elevation localities at southern end of range and again between 8° and 10°N reflects low elevations of Andes in those regions. However, absence of almost any specimens of either species below 2,500 m in dept. Huila from about 2°N to over 4°N (ca. 250 km) and again between 8° and 10°N apparently reflects major gaps in collecting efforts. Low-elevation localities for *B. torquatus* north of 10°N represent subspecies *B. t. perijanus*, a member of *torquatus* group of subspecies, whereas those below 1,500 m at midlatitudes represent *B. t. atricapillus*.

*torquatus* has been recorded at high elevations south of about 5°N, but not north of about 6°. Thus, different slopes of the same mountain range seem to show different patterns, although gaps in sampling effort leave open the possibility that the differences are an artifact. Two species have been collected at the same locality at only 1 (2.6%) of 39 sites (La Bodega, dept. Antioquia).

On the eastern slope of the Western Andes in Colombia (Fig. 6), *B. torquatus* is known only from one locality below 2,500 m and from three widely separated localities above 3,000 m; the low elevations of the summits of the Western Andes in the intervening areas evidently create this gap at high elevations. Lower elevations are occupied by *B. brunneinuchus*, including elevations inhabited by *B. t. atricapillus* elsewhere in northern Colombia, although there appears to be a major gap in sampling at middle latitudes, just as for species of *Atlapetes* (Remsen and Graves 1995). The two species have been collected at the same locality at 1 (5.6%) of 18 sites (Cerro Munchique, dept. Cauca).

On the western slope of the Western Andes of Colombia, Ecuador, and northern Peru (Fig. 7), *B. brunneinuchus* occupies elevations mainly below 2,100 m from north of 6°N south to almost 4°S (prov. Loja, Ecuador). At higher elevations near the Equator in Ecuador, *B. torquatus* is found, but it is not found north of this, where the Western Andes do not rise much above 2,200 m. Where *B. brunneinuchus* drops out south of about 4°S, *B. torquatus* expands its elevational range downwards to the lower limits of montane forest. At about 3°45'N, a low-elevation population of *B. torquatus* (*B. t. atricapillus*) is found that may replace *B. brunneinuchus* at low-elevations north of this latitude, but locality data are absent. The two species have been collected at the same locality at only 1 (0.9%) of 114 sites (Nieblí, prov. Pichincha, Ecuador).

#### DISCUSSION

Because the gaps in distribution of *B. torquatus* contain the same general habitat inhabited by the species throughout its range, namely mon-

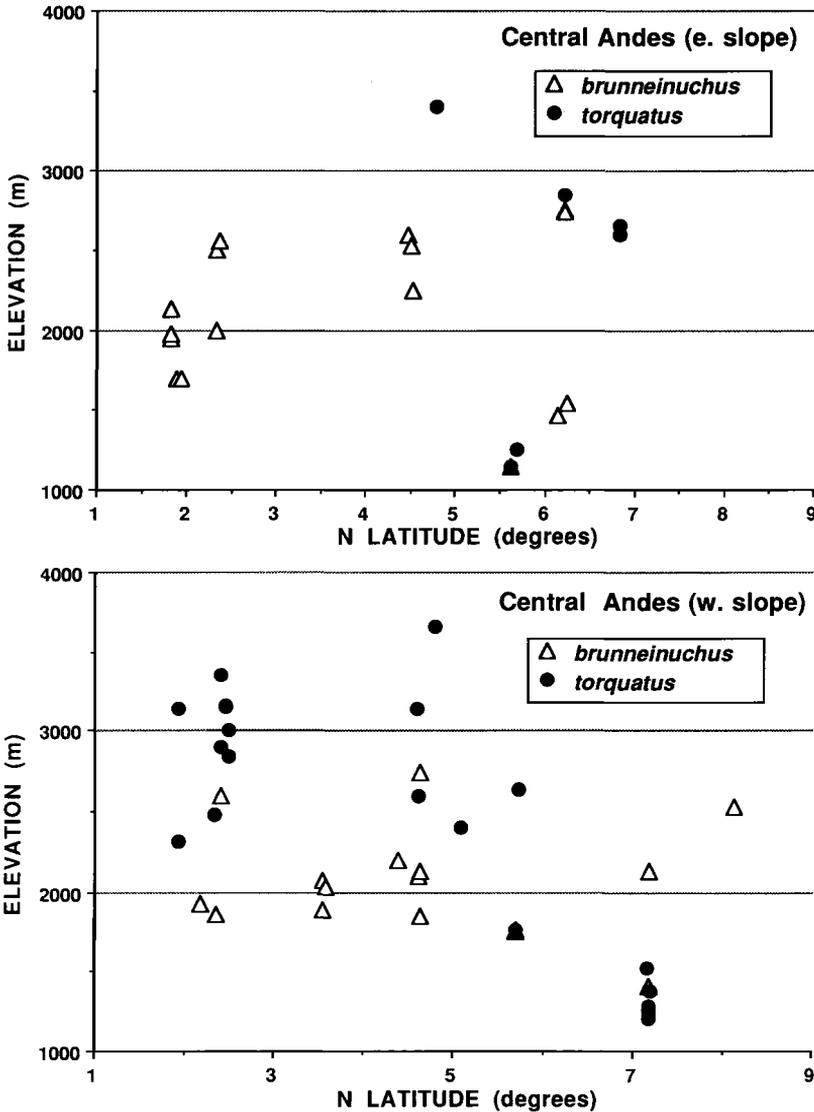


Fig. 5. Distribution of species of *Buarremon* in Central Andes of Colombia. Each point represents locality from which one or more specimens obtained.

tane forest edge, it seems highly unlikely that its absence from the gaps is caused by habitat unsuitability or other autecological factors. Habitat differences along the elevational gradient within areas inhabited by *B. torquatus* appear to be much greater than those between similar elevations within and outside its latitudinal range. In other words, because *B. torquatus* is found in habitats from cold, stunted, depauperate timberline forest to warm, high-canopy, species-rich forest at the lower limit of montane bird distribution, it seems unlikely that

the absence of some critical ecological requirement accounts for its absence at identical elevations at adjacent latitudes. 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 most of their latitudinal range (Remsen and Cardiff 1990). Although habitat suitability has not been studied at elevations with and without *B. torquatus* or *B. brunneinuchus*, the relative uniformity of elevational

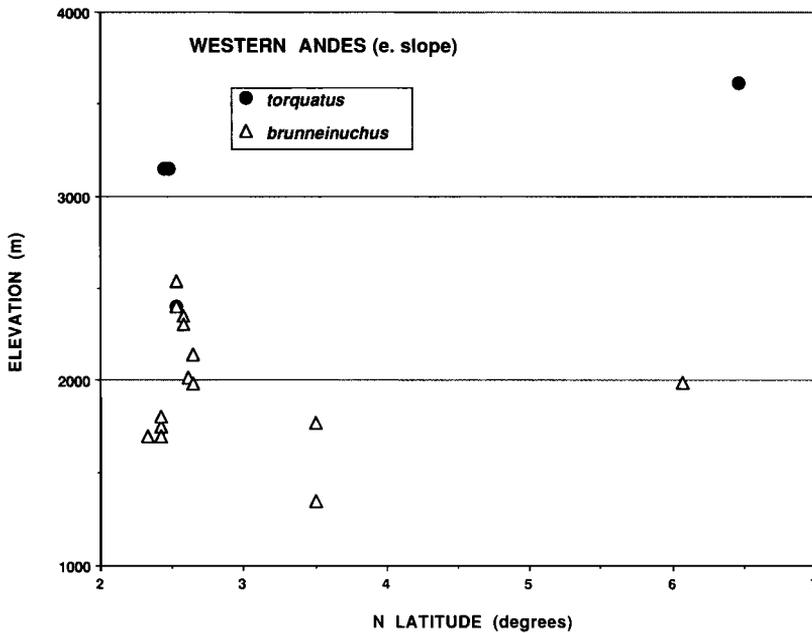


Fig. 6. Distribution of species of *Buarremon* on eastern slope of Western Andes of Colombia; each point represents locality from which one or more specimens obtained. Absence of any specimens from about 3°30'N in northern dept. Valle to about 6°N in central dept. Antioquia (ca. 300 km) apparently indicates major gap in collecting efforts, one of largest in Andes.

limits of Andean birds indirectly supports the notion of uniformity of habitat. Therefore, we think that habitat differences do not influence the presence of gaps in distribution.

The complementary distributions of *B. brunneinuchus* and *B. torquatus* throughout the Andes provide circumstantial evidence for the importance of interspecific competition in governing their distributions. This pattern only becomes evident when elevation is considered along with latitude. Wherever the two species are found at the same latitudes, they occupy separate elevational distributions, with *B. torquatus* usually but not always (e.g. Venezuela and northern Andes of Colombia) the higher-elevation species. Where only a single species is found (e.g. Santa Marta Mountains, most of Venezuelan Andes, western slope of the southern Western Andes, and eastern Andes of Bolivia), that species usually occupies the entire range of elevations. Although *B. torquatus* typically is the high-elevation form, the relative elevational positions of the two species are reversed in the many areas of the Andes of northern Colombia and in most of the Venezuelan Andes (as well as in an area, the Coastal Range of Venezuela, that we did not analyze; Schafer and Phelps

1954); such "niche switches" provide strong evidence that the elevational limits of the two species are not governed by autecological factors (Remsen and Cardiff 1990). That either species can occur from timberline to the lower limit of cloud forest strongly suggests that where one shows narrower elevational distributions, such a constriction is not the result of inability to adapt to the entire range of ecological or physiological conditions along the elevational gradient. Therefore, we interpret the pattern of distribution of these two species to indicate that their elevational limits are determined by interspecific competition. Their pattern of distribution is similar to that shown by *Melidectes* honeyeaters in montane New Guinea by Diamond (1973), who outlined the rationale for interpreting such patterns as the products of the process of interspecific competition. Unfortunately, experimental manipulations that would directly test the interspecific-competition hypothesis are impractical in such field situations (Diamond 1986).

Of the 567 specimen localities in mountain ranges where both species of *Buarremon* occur, the two have been recorded together at only 9 (1.6%) sites, all of which are at elevations where

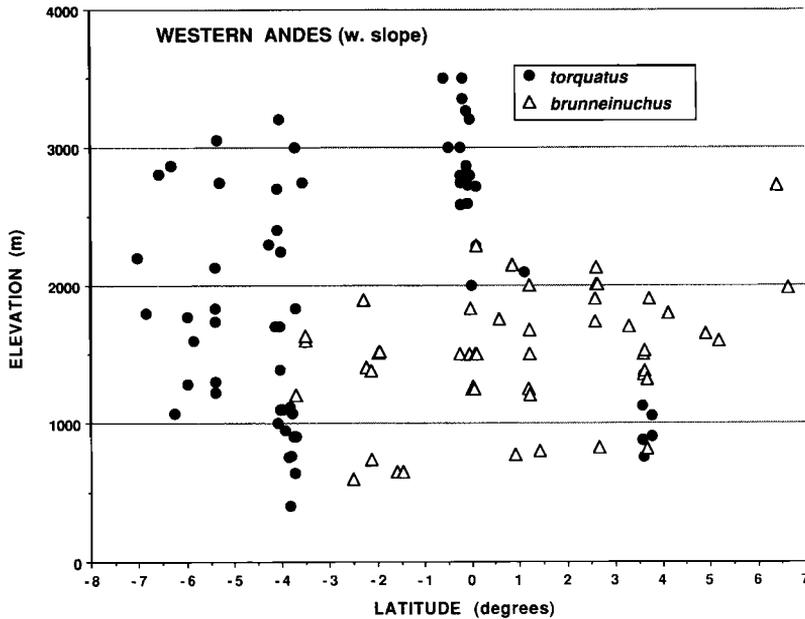


Fig. 7. Distribution of species of *Buarremon* on western slope of Western Andes from Colombia to northern Peru; each point represents locality from which one or more specimens obtained. "Negative" latitudes are those south of Equator.

the two species' ranges about. As noted by Remsen and Cardiff (1990) and Remsen and Graves (1995), we could not determine from the specimen data whether this apparent overlap represents true syntopy or whether there were local differences at a given collecting locality in elevations or slopes where the two species were collected. A collecting locality typically includes a variety of slopes and elevations within walking distance of camp. F. G. Stiles (in litt.) has noted that, where the two species overlap on his study area in Colombia, *B. torquatus* is found in dense bamboo thickets, whereas *B. brunneinuchus* is found in forest understory. Detailed sampling, particularly along a transect in those areas of the Colombian Andes where *B. brunneinuchus* is sandwiched by *B. torquatus*, with special attention to habitat use where two forms come together, would contribute greatly to our understanding of the determinants of distribution of these species.

The importance of interspecific competition in determining range limits is highly controversial (Wiens 1989). Terborgh and Weske (1975) interpreted comparative elevational distributions from two localities in Peru to indicate that interspecific competition plays a prominent role in determining elevational limits of Andean

birds, including up to 71% of the species in their analysis. The accuracy of their data set and interpretations from it have been challenged only by Graves (1985) and Wiens (1989), who pointed out some of the unavoidable problems in sampling such complex areas and in comparing results from different areas. Because the Terborgh-Weske data set has provided the only quantitative support for widespread influence of interspecific competition in elevational distributions of Andean birds, and because their interpretations of their data set have recently been presented in textbooks (Faaborg 1988, Gill 1990), we here present a critique of this data set.

Although we agree that interspecific competition plays a role in the distribution of some Andean bird species (Remsen and Cardiff 1990, Remsen and Graves 1995), we question whether available data show that this role is as prominent as Terborgh and Weske portrayed. They used the higher upper-elevational limits shown by 46 species in the isolated Cerros del Sira as evidence that many species expanded their ranges upward in response to the paucity of montane species in the Sira. Inspection of their data, however, reveals that 16 (35%) of these 46 species increase their upper limit by less than

100 m, and some by as little as 15 to 25 m, roughly one-half the distance from the ground to the canopy. In our opinion, such minute "expansions" are beyond the limit of the resolution of the data and are well within the range of measurement error of most altimeters. Another eight species (17%) expanded their ranges upward by only 100 to 200 m, and five (11%) by 200 to 300 m; again, we question whether such distances are either real or meaningful with respect to interspecific competition (versus aut-ecological factors). For example, the upper and lower limits of Andean cloud forest vary by at least 300 m within a region, depending on local climatological and topographical conditions (Chapman 1917, Graves 1985); in fact, upper and lower elevational limits differed by as much as 300 m for the same species on different slopes of the Cordillera Vilcabamba itself (Weske 1972: appendix 1).

Terborgh and Weske (1975) noted that such local differences between the Sira and the Vilcabamba were responsible for a 300-m downward displacement in elevation of ecotone boundaries in the Sira. If this is the case, then a 15-m upward elevational shift in a bird species' distribution there would actually correspond to a 315-m upward shift, probably a meaningful difference. Conversely, however, only 2 of the 10 downward shifts in elevational distribution attributed to competitive release by Terborgh and Weske were of more than 300 m. Clearly, interpretation of elevational shifts in distribution transposed upon displacements of environmental zones creates a situation that makes interpretation complex.

Expansion of elevational ranges in the absence of ecologically comparable congeners provided Terborgh and Weske (1975) with their most convincing examples of ecological release. However, of the 18 such species in the Sira, the expansion was more than 300 m for only 6 (33%). Of these six species, difficulties in detection make determining precise elevational limits problematic for three: *Otus ingens* (nocturnal owl), *Scytalopus femoralis* (secretive, terrestrial species infrequently captured by mist nets), and *Lepidocolaptes albolineatus* (canopy species virtually never captured by mist nets). This leaves only three species (*Heliodoxa leadbeateri*, *Pseudotriccus pelzelni*, and *Hemispingus frontalis*) with what we would consider substantial and undeniable upward range expansions in the absence of a congener.

Terborgh and Weske (1975) did not point out that upper limits in the Sira for 10 species were actually lower than those in the Vilcabamba in spite of the absence of a congener in the Sira: *Glaucidium minutissimum*, *Malacoptila fusca*, *Aulacorhynchus derbianus*, *Veniliornis affinis*, *Pipreola frontalis*, *Ochthoeca pulchella*, *Myiodynastes maculatus*, *Leptopogon superciliaris*, *Cacicus cela*, and *Buarremon brunneinuchus*. Overall, of the 246 species' elevational limits analyzed in the Sira, 103 (42%) actually showed lower upper-limits there than in the Vilcabamba. Presumably, Terborgh and Weske (1975) would attribute this to the downward displacement of environmental zones there.

In the Cordillera Vilcabamba, Peru, Terborgh (1971) used abutting elevational distributions of congeners as evidence for interspecific competition. Valid comparisons must represent species that are likely competitors. Three (*Cacicus*, *Grallaria*, and *Xiphorhynchus*) of the 10 examples of groups of congeners graphed by Terborgh contain unlikely candidates for competitors. *Cacicus holosericeus* is not the ecological equivalent of *C. leucoramphus*; *C. holosericeus* is a secretive species of dense undergrowth, primarily bamboo, whereas *C. leucoramphus* feeds in the canopy (Remsen 1985, Ridgely and Tudor 1989, Fjelds  and Krabbe 1990, Kratter 1993); furthermore, they overlap widely in elevational distributions and are syntopic elsewhere in their ranges (e.g. Remsen 1985). Three of the four species of *Grallaria* differ dramatically in body size (*G. rufula* ca. 35 g, *G. guatemalensis* and *G. erythroleuca* ca. 85 g, and *G. squamigera* ca. 130 g), and all four are difficult to detect by netting or visual observations, making their elevational limits difficult to determine without knowledge of vocal differences. *Xiphorhynchus ocellatus* and *X. guttatus*, which also differ dramatically in body size, are not only syntopic elsewhere (e.g. Terborgh et al. 1984), but differ in substrate use, especially in degree of use of hanging dead leaves (Remsen and Parker 1984, Chapman and Rosenberg 1991); only *X. ocellatus* and *X. triangularis* are likely competitors. Graves (1985) also pointed out that, in addition to the *Cacicus* and *Grallaria* examples, two other sets of congeners (*Coeligena* and *Thripadectes*) noted by Terborgh as having nonoverlapping distributions in the Vilcabamba in fact overlap elsewhere.

We believe that the Terborgh-Weske data provide less support for the importance of interspecific competition in determining eleva-

tional distributions of Andean birds than Terborgh (1971) and Terborgh and Weske (1975) judged. Although we suspect that abutting elevational distributions of ecologically similar congeners that do not coincide with ecotone boundaries are more likely explained by interspecific competition than by autecological thresholds, we think that, minimally, "natural experiments," such as absence of one of the species from portions of the other species' range (e.g. Remsen and Cardiff 1990, Remsen and Graves 1995), must be analyzed before invoking interspecific competition. Terborgh's natural experiment, the Cerro Sira, provided only limited support. Although we interpret the pattern of distribution shown by species of *Buarremon* to be explained best by interspecific competition, we consider the role of interspecific competition in determining elevational distributions of most Andean birds to be unresolved.

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