59.88.1B:11.52.4

Article IX.—MUTATION AMONG BIRDS IN THE GENUS BUARREMON

By Frank M. Chapman

PLATES XIV TO XVII

The question of mutation vs. the direct action of environment has recently claimed the attention of ornithologists.¹ Most of those who have expressed themselves in print seem to favor one or the other of these factors, whereas it seems to me that both may be operative. With enormous series of wide-ranging species at his command, the ornithologist is in possession of material to determine the character and extent of the variations in color and in size exhibited by what is obviously the same When to this intensive laboratory investigation he adds a knowledge of the environmental conditions under which the species exists, he can often definitely correlate effect and cause.

Thus, he finds large forms occupying colder areas, dark ones humid areas, and pale ones arid areas; and as the conditions which obviously produce these variations in size and color merge one with the other, so do the forms themselves intergrade. That these variations are inherent and not merely the temporary impress of environment on the individual is apparently shown by the fact that they are often as well marked in the nestling as in the adult.

While my experience as a collector and "museum man" has convinced me of the profound influence exerted by observable environmental factors (chiefly climatic) on the species, it has also brought to my attention certain instances in which I believe species have arisen by what is termed mutation, that is, the appearance of characters, great or small.² which

an attempt to determine their nature and their causes.

I take advantage of this opportunity to endorse Professor Morgan's "pious wish" (loc. cit., p. 238) for coöperation between geneticists and systematists. After all, both are trying to discover real relationships and if the latter from the nature of their material, the limitation of their methods, and the classifiers' necessity of always making some decision not infrequently reach erroneous conclusions, their handicaps should win for them the assistance rather than the criticism of those who are discovering more certain means for the determination of affinities than are afforded by most museum specimens.

¹Lowe and Mackworth-Praed, Ibis, 1921, pp. 344-347; Meinertzhagen, idem, pp. 528-537; Bonhote, idem, pp. 720-725; Haviland, idem, pp. 752-754; idem, 1922, pp. 712-715.

'The following quotation from an article by Prof. T. H. Morgan, which has appeared since this paper was written, is unusually pertinent in this connection:

"But we also know that minute differences also arise as mutants, and that these are inherited in the same way as are the larger mutant changes. It is also now clear that these smaller mutant variations must be those small heritable variations that Darwin himself appealed to as furnishing the materials for organic evolution. In these respects we have made great advances in knowledge since Darwin wrote; and I doubt if a single geneticist familiar with the evidence at first hand will hesitate to make this substitution. We have learned to distinguish between those individual differences due to the environment (that are not inherited) and those that arise as mutantions (that are inherited). Superficially there is no way of telling one from the other, since they overlap and involve the same changes in the same characters. But by pedigree work the essential difference can be made evident, as Johannsen demonstrated in 1909." (Scientific Monthly, XVI, No. 3. 1923, pp. 237-246).

"Pedigree work," except with domesticated species, is rarely possible with birds, and such contributions as the ornithologist can make to this subject from a study of birds in nature must be based on the examination of a sufficient number of specimens fully to illustrate the range of a species' variations with an attempt to determine their nature and their causes.

apparently are the expression of an inherent tendency to vary rather than of environment. Such characters are commonly termed "individual variations." They may be manifested by a greater or lesser number of individuals in widely separated parts of the range of the species, and their perpetuation evidently depends upon their frequency and, especially, on an environment which affords sufficient isolation to ensure their preservation.

To determine the causes which create the inherent tendency to vary regardless of environment is a problem which lies within the field of the experimental biologist. We have here only to consider their results.

To this end I present here the results of my researches, in the museum as well as in the field, of the species of the genus *Buarremon*, together with the conclusions which I have ventured to draw from them.

Briefly, we have two groups of birds in the genus Buarremon, the members of which are distinguished from one another, primarily, by having a chestnut or a black and gray or black crown and, secondarily, by the presence or absence of a black pectoral band. It is this black collar which is the principal mutant character and which, as I shall attempt to show, appears or disappears purely as an individual variation and without relation to external influences. Its perpetuation or establishment as a specific mark does, however, depend upon environment expressed in what is doubtless the most important external agent in promoting evolution—that is, isolation.

I do not wish to confuse the main issue by presenting too many details. Since, however, mutation as a species-making agent among birds is not generally accepted, it seems desirable to give here all the facts at my command for the consideration of those students who are not prepared to agree with my conclusions.

Furthermore, if my interpretation of these facts is approximately correct, I believe that it will afford a clue to the origin of many types of distinguishing marks among birds the existence of which it is difficult to attribute to even indefinitely prolonged action of external causes.

The two groups of birds with which we are concerned are the following:

GROUP I. (CROWN CHESTNUT)

Section A. (Pectoral Band Present)

Buarremon brunneinuchus

Subtropical Zone, southern Mexico to southern Peru.

Section B. (Pectoral Band Absent)

Buarremon inornatus

Subtropical Zone, Chimbo Valley, western Ecuador.

¹Including also an allied species (*Pipilo torquatus*), which possesses characters commonly accorded generic rank.

GROUP II, (CROWN BLACK OR BLACK AND GRAY)

Section A. (Pectoral Band Absent)

Buarremon assimilis assimilis.

Temperate Zone, western Venezuela, Colombia and Northern Ecuador.

Buarremon assimilis nigrifrons.

Subtropical Zone, southern Ecuador and northern Peru.

Buarremon assimilis costaricensis.

Subtropical Zone, southwestern Costa Rica.

Buarremon atricapillus atricapillus

Subtropical Zone, northern end of Central Andes, Colombia.

Buarremon atricapillus tacarcunæ.

Subtropical Zone, eastern Panama.

Buarremon virenticeps.

Southern end of Mexican tableland.

Buarremon borelli.

Northern Argentina.

Section B. (With a Pectoral Band)

Buarremon basilicus

Subtropical Zone, Santa Marta Mountains.

Buarremon phæopleurus.

Subtropical Zone, Caracas region.

Buarremon phygas.

Mountains of northeastern Venezuela.

Buarremon poliophrus.

Temperate Zone, eastern Central Peru.

Buarremon torquatus

Subtropical Zone, Yungas region, Bolivia.

Buarremon fimbriatus

Subtropical Zone, "ravine near Mizque," Bolivia.

THE FIRST GROUP

Buarremon brunneinuchus, a tanagrine finch, is found throughout almost the entire Subtropical Zone from Mexico to Peru, a more extended range, I believe, than that of any other subtropical species. But, in spite of this fact, no race of it is recognized by systematists, excellent evidence that it presents no appreciable geographic variation. In the Chimbo Valley of western Ecuador, however, it is represented by a closely allied but apparently specifically distinct form, Buarremon inornatus, and this bird I believe to be a mutant of brunneinuchus.

In the color of the upperparts the two birds are exactly alike, olivegreen with a rufous-chestnut crown and black forehead and cheeks. Below, *inornatus* has the white areas larger, and it lacks the conspicuous black breast-band which distinguishes *brunneinuchus*.

I have met the last-named species in life in Mexico, Colombia, and Peru, but a field acquaintance with *inornatus* and its haunts seemed essential to a satisfactory consideration of the relationships of these two birds. This acquaintance it was my privilege to make in August, 1922.

The following facts in relation to the ranges, characters, variations, etc., of these species, are based on a study of 137 specimens contained in the American Museum, sixteen kindly loaned me by Dr. J. Dwight and Dr. Witmer Stone, and five in the British Museum.

Buarremon brunneinuchus (Lafresnaye)

DISTRIBUTION.—Buarremon brunneinuchus is found throughout the Subtropical Zone (or usually between the altitudes of 4–5000 and 9000 feet) from the Province of Vera Cruz, Mexico, to southeastern Peru, except in the Santa Marta Mountains of Colombia and the Chimbo-Chanchan drainage system of western Ecuador. In the latter place it is replaced by Buarremon inornatus. With many other species or representative forms common to the Subtropical Zone of Costa Rica and Chiriqui and eastern Panama and Colombia, it is lacking in the region between western and eastern Panama where the mountains fall below the altitude which here marks the lower limit of the Subtropical Zone, and it is doubtless also absent from other regions in which the Subtropical Zone is wanting. In short, expressed graphically, if somewhat loosely, the range of Buarremon brunneinuchus may be said to be some 5000 miles long and a mile wide.

In view of its wide distribution, its apparent absence from the Santa Marta Mountains of Colombia is significant, and the fact that it is wanting in the Chimbo-Chanchan valleys, where it is replaced by *Buarremon inornatus*, indicates that the latter represents it in that locality. We have specimens from Mindo and from El Chiral, respectively north and south of the range of *inornatus* on the western slope of the Ecuadorian Andes.

Habits.—Buarremon brunneinuchus lives on or near the ground in the dense, luxuriant undergrowth of the Subtropical Zone. It is usually seen along the borders of trails or clearings either because it or the collector selects such situations. Its habits in a general way resemble those of the towhee (Pipilo erythrophthalmus) but it is more retiring than that bird, frequents denser growth, and does not range as far above the ground. It is by no means shy and is sufficiently curious to be attracted by the collector's "squeaking," or imitation of the notes of a bird in distress, a fact which has permitted the forming of adequate series of specimens of a species which, if it were wary, would be exceedingly difficult to secure.

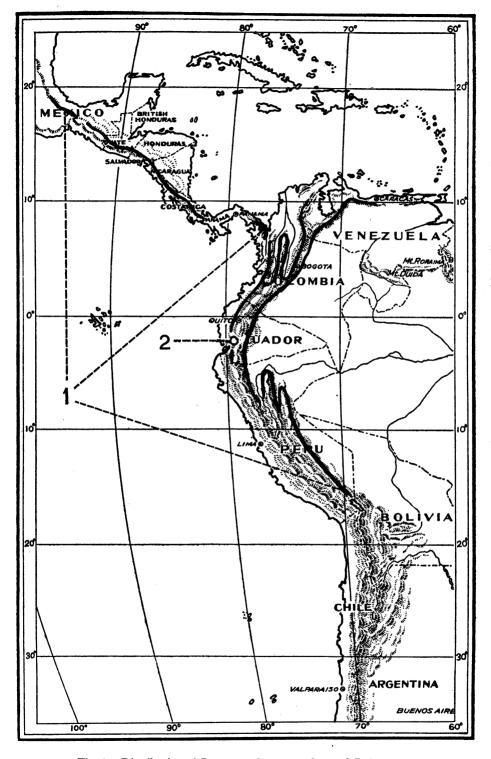


Fig. 1. Distribution of Buarremon brunneinuchus and B. inornatus.

Range of Buarremon brunneinuchus in the Subtropical Zone from Mexico to southern Peru.
 Range of Buarremon inornatus in the Chimbo Valley of western Ecuador.

Its call-note, which Stolzmann¹ describes as "tsit-tsit," is not often uttered, and its song, which I have never knowingly heard, is described by the same author as resembling the cry of a rubber doll!

The nest, according to Stolzmann (loc. cit.) and Carriker,² is placed in low bushes and the eggs, according to the last-named author, are pale bluish white, unmarked.

Characters of the Adult.—Buarremon brunneinuchus is a tanagrine finch about 190 mm. (7½ in.) in length, with the short rounded wing and stout feet of a terrestrial, sedentary bird. In color it is largely olive-green above, with white underparts and a black band across the breast; the forehead and sides of the head are black, with small white marks above the lores and at the base of the culmen; the crown is chest-nut-rufous, with a narrow lateral border of ochraceous-orange from above the eye to the nape; the wings and tail are fuscous, edged with olive-green and with bright yellow on the bend of the wing; the sides and flanks are grayish, more or less washed with olive-green; the under tail-coverts are olive-green, usually tinged with brown; and there is often more or less gray on the breast posterior to the black pectoral band.

This description is presented merely to show that both the color and the pattern of *Buarremon brunneinuchus* are sufficiently diversified to offer an opportunity for the display of those variations which it is usual to ascribe to the influence of climatic environment.

Variations

Variations with Age.—The juvenal plumage is sooty olive, with a few yellowish streaks on the abdomen, the wings and tail resembling those of the adult. The crown is tinged with dark brown, with a paler lateral margin, suggesting the color and pattern of the adult plumage, but the throat is blackish, darker, therefore, than the remaining underparts; the lower mandible, in three of four specimens, is wholly or largely horn-color or brownish. At the post-juvenal molt the wings and tail are retained, but the rest of the plumage is replaced by that of the adult, from which, at the completion of the molt, the young bird in its "first winter" plumage cannot certainly be distinguished, though in some specimens the lower mandible remains horn-color. It should be noted that the pectoral band is apparently as well developed by this post-juvenal molt as in older birds.

¹Orn. du Pérou, II, p. 530. ²1910, Ann. Carnegie Mus., VI, p. 899.

Sexual Variation.—There is no apparent sexual variation in color, but in size males average larger. Eight males and five females from the Western Andes of Colombia measure as follows:

	Wing	TAIL	Tarsus
8 males	81-85	80-86	29-31
5 females	78-81.5	77.5-81	29-30

Seasonal Variation.—Forty-one specimens from Colombia (western and Central Andes and western slope of the eastern Andes) represent every month in the year except August. The breeding season, however, evidently extends throughout the greater part of the year and any attempt to determine the yearly range of variation in the color of the plumage of adult specimens must clearly, therefore, be based on the comparison of specimens in similar stages of plumage.

Dissection shows that specimens taken in January, February, March, April, May, June, October, November, and December were breeding. Doubtless this extended nesting season is in part due to local variations in the time of the wet seasons; but the capture of young in juvenal plumage on the western slope of the Central Andes above Palmira in April, and at Salento in September, shows that even under essentially similar climatic control the breeding season covers not less than six months.

Making due allowance for this fact, I am still unable to discover any appreciable seasonal variation in color in this species. In spite of its terrestrial habits, its plumage becomes but little worn, and the nature of its haunts prevents it from being exposed to the sun or to strong light. Freshly plumaged birds show traces of white edgings on the black pectoral band, and their flanks may average greener, but these characters are slight and not constant.

Geographic Variation.—The fact that, in spite of its wide range, no geographic races or subspecies of *Buarremon brunneinuchus* are recognized by systematic ornithologists is an eloquent tribute to the stability of the bird's characters. In color, specimens from Jalapa, Mexico, at or near the northern limit of the bird's range, have more gray on the underparts than most specimens from farther south, but they can be matched by others from Chiriqui and Colombia. An excellent series from Nicaragua agrees closely with average South American specimens both in the amount of gray on the underparts and in other respects.

Ridgway,¹ with a series of thirty-eight specimens, including not less than twelve from southern Mexico, states that he is "unable to detect any color differences that can be correlated with geographic areas."

In size, as in color, this species is notably constant, as the appended table of measurements of thirty males from throughout the range of the species shows. In the mountains of eastern Panama the tail appears to be proportionately shorter than elsewhere, while specimens from southwestern Ecuador average smaller than others in the series.

The bill shows a slight local variation and averages slightly larger and more slender in specimens from near Mérida, Venezuela, and somewhat shorter and proportionately stouter in those from western Ecuador.

MEASUREMENTS OF MALES OF Buarremon brunneinuchus

	Wing	TAIL	Culmen
Jalapa, Mex.	83.5	85.0	18.2
u u	84.0	84.0	18.0
Matagalpa, Nicaragua	85.0	81.0	18.0
""""	81.5	78.0	18.0
u u	86.0	84.0	19.5
Boquete, Chiriqui	83.0	80.0	18.0
<i>"</i> " " <i>"</i>	82.0	80.0	17.5
" "	83.0	82.0	17.5
"	83.0	84.0	18.0
Tacarcuna, E. Panama	83.5	79.0	18.0
" "	82.0	76.0	18.5
" "	83.0	78.0	19.0
u u	83.0	79.0	18.0
San Antonio, W. Andes, Col.	85.0	83.0	17.5
<i>"""</i>	81.5	81.0	18.5
" "	85.0	82.0	19.0
u u u	83.0	81.0	18.5
<i>u u u</i>	84.0	87.0	19.0
Mérida, Venezuela	81.0	85.0	19.5
" "	85.0	86.0	19.0
Macas, E. Ecuador	82.0	77.0	18.0
"	85.0	81.0	18.5
Zamora, E. Ecuador	86.0	83.0	18.0
Mindo, W. Ecuador	83.0	82.0	17.0
El Chiral, W. Ecuador	80.5	78.0	17.5
"	81.0	77.0	18.0
Near Zaruma, W. Ecuador	80.5	78.0	17.0
u u u			17.0
Utcuyacu, Junin, E. Peru	81.5	78.0	18.0
Torontoy, E. Peru	83.0	85.0	18.0
<i>u</i> = <i>u</i>	81.0	78.5	17.5
"	83.0	84.0	18.0
Santo Domingo, Southeastern Peru	80.0	81.0	18.0

POSTMORTEM VARIATION IN COLOR.—Under this head I refer only to those changes which occur in specimens of certain birds the exact cause of which is not clearly understood but the extent of which depends upon the age of the skin. Thus, comparison of old "Bogotá" skins collected not less than forty or fifty years ago with others recently collected in the Bogotá region (above Fusugasugá and Buena Vista above Villavicencio) shows that in the older specimens the wings and tail are browner, the back lighter, more vellow-green, the black areas duller. Similar but less pronounced differences exist between specimens collected by de Oca at Jalana about 1870 and several collected at the same locality by myself The latter, however, are paler than specimens collected by Miller and Griscom in Nicaragua in 1917, and doubtless have faded since they were prepared. It is obvious, therefore, that in this species. as in many others, due consideration must be given the age of the specimens when making comparisons. It is, of course, understood that in every instance these specimens have always been stored in light-proof cabinets.

Individual Variation.—The variations in the color of Buarremon brunneinuchus which cannot apparently be ascribed to age, sex, season, or environment are limited chiefly to the amount of greenish wash on the gray sides and of a brownish tinge in the lower tail-coverts. In pattern of Marking, including extent of area occupied by certain colors, the variation is greater. Thus, the black band on the forehead ranges from 7 mm. to 12 mm. in width, from the base of the culmen, and rarely its median white line is wanting. In the intensity of the olive-green of the upperparts there is practically no individual variation, but there is a pronounced variation in the amount of gray on the underparts and, particularly, in the width of the black pectoral band.

As has been stated, our Mexican specimens average grayer below than those from farther south, but, aside from this possible geographic variation, there is also much variation among individuals from the same locality in this respect. For example, in a series from Boquete one male is largely gray, another largely white in the region posterior to the black pectoral band. It is, however, in the pectoral band itself that the greatest variation is found. Thus, in a female from Las Lomitas, in the western Andes of Colombia, this band measures approximately 5 mm. in width, whereas in a female from Cerro Munchique, in the same range, it has a width of 11 mm. Again, in males from Chiriqui the band varies from about 5 mm. to 15 mm. in breadth. There is almost as much variation in its lateral extent as in its width. In some specimens it is confluent

with the black of the sides of the head, though usually separated from it by the gray of the sides of the breast or white of the throat.

Variation in this character reaches its extreme in an adult female from Ricuarte, Colombia, in which the pectoral band is not only very narrow but not continuous, the feathers forming its central portion being in part white.

Berlepsch and Taczanowski¹ state that a specimen in the Warsaw Museum, acquired from the elder Verreaux, named by Jules Verreaux "Buarremon brunneinuchus," and labeled "Mexico" resembles a specimen of inornatus from Cayandeled, Ecuador. It has no trace of a black collar but in size resembles brunneinuchus.

Prior to the time in which these authors wrote, *B. inornatus* was known authentically only from the specimens in the British Museum secured by Fraser at Pallatanga in 1858. I am familiar with no record of collections made in the Chimbo Valley between the visit of Fraser and that of Stolzmann and Siemiradski, on whose work Berlepsch and Taczanowski were writing in 1884. This fact, in connection with the statement that the specimen resembles *brunneinuchus* in size, indicates that it is an example of that species in which individual variation in the pectoral band is carried to an extreme, rather than a specimen of *inornatus*; in other words, it is a mutant.

Summary

- 1.—Buarremon brunneinuchus ranges throughout the Subtropical Zone from Mexico to Peru. It is wanting in the Santa Marta Mountains of Colombia and in the Chimbo Valley of western Ecuador, though found both north and south of that valley in western Ecuador.
- 2.—It is a terrestrial, sedentary inhabitant of heavily forested regions. The sexes are alike in color, the male being slightly larger. The adult plumage, which is acquired at the post-juvenal molt, is varied in color and in pattern, and presents practically no variations with age or season.
- 3.—Notwithstanding its exceptionally extended range, the bird exhibits no appreciable variation in color or size which can be correlated with any given area. Fading in color occurs in museum specimens even when they are not exposed to light, its amount depending on the age of the specimen.
- 4.—Pronounced individual variation is manifest in the extent of the gray or grayish olive areas of the sides and flanks, of the gray on the breast, and in the width and extent of the black pectoral band.

¹1884, Proc. Zoöl, Soc., London, p. 292.

Buarremon inornatus Sclater and Salvin

DISTRIBUTION.—Subtropical Zone in the Chimbo-Chanchan river system of western Ecuador in the following localities:

Prov. Chimborazo: Pallatanga, 4950 ft. (3, Brit. Mus.); Cayandeled, 4500 ft. (1, Berlepsch Coll.); Junction Chanchan and Chiguancay Rivers, 2500 ft. (3, Acad. Nat. Sci. Phila.); Pagma Forest, 7200 ft. (3, Acad. Nat. Sci. Phila.); Rio Chimbo, 2800 ft. (2, A. M. N. H.); Pallatanga, 4200 ft. 1; 5000 ft., (1, A. M. N. H.). Prov. Bolivar: Porvenir (1, Brit. Mus.). A specimen in the British Museum is recorded in the 'Catalogue of Birds,' as "Jima, Ecuador (Buckley)," but, as Jima is in the Temperate Zone of eastern Ecuador, it is evident that this specimen is among the unfortunately large number of inaccurately labeled birds in the Buckley collection.

The Chimbo separates a spur of the western Andes from the main mountain range. While this spur, known as the Chillanes range does not reach a greater altitude than 8000 ft., it is evident from collections made by Fraser¹ at Chillanes that, in spite of the comparatively low altitude, the fauna of the summit of the range is strongly humid temperate in character, a fact possibly due to the proximity of the snowfields of Chimborazo. This condition creates a measure of isolation in the Valley of the Chimbo and its tributaries which apparently has been sufficiently effective to permit of the development of the characters which distinguish Buarremon inornatus from B. brunneinuchus.

GENERAL Habits.—In habits and choice of haunts Buarremon inornatus resembles B. brunneinuchus. I am not familiar with, and know of no description of its call-notes, song, or nest and eggs.

Characters.—In the rufous-chestnut crown, bordered with ochraceous-orange, black forehead and sides of the head, olive-green back, etc., *inornatus* exactly resembles *B. brunneinuchus*, but the underparts have more white, the black breast-band is absent, and its size is slightly smaller.

Measurements

	$\mathbf{W}_{\mathbf{ING}}$	TAIL	Culmen
Pallatanga, Ecuador, &	74.0	73.0	18.0
Pagma Forest, Ecuador, ♂	74.0	72.0	17.5
Rios Chanchan and Chiguancay, Ecuador, &	79.5	75.5	18.3
Rios Chanchan and Chiguancay, Ecuador, o	79.0		18.3
Rios Chimbo and Coco, Ecuador, Q	75.0	73.0	17.3
Rios Chimbo and Coco, Ecuador, Q	77.0	73.0	17.3
Rios Chimbo and Coco, Ecuador, Q	74.0	71.0	
Pagma Forest, Ecuador, Q	74.0	72.0	18.0

Variations.—Of the sixteen specimens of Buarremon inornatus known to me. I have examined all but the male from Cavandeled in the Berlepsch Collections. The juvenal plumage, if one may judge from a Pallatanga specimen in the British Museum, resembles that of B. brunneinuchus. The sexes are alike in color, but the males average slightly larger in size. The range of the species is too limited to expect it to exhibit appreciable geographic variation, but individually it varies in the extent of encroachment of the greenish gray sides on the white of the underparts and the degree to which a pectoral band is suggested by black-marked feathers on the breast. An adult male in the American Museum taken by George Cherrie, July 31, 1922, has the grayish green sides even more extensive than in average specimens of brunneinuchus, while across the breast there are unmistakable traces of a pectoral band. Of six specimens collected by S. N. Rhoads, in the Academy of Nat. Sci. Philadelphia, a male from the junction of Chanchan and Chiguancay rivers has several black-marked feathers in the center of the breast: a second male from the same locality and a male from Pagma Forest show traces of black at the sides of the breast.

Summary

- 1.—Buarremon inornatus occupies a limited area in the Subtropical Zone of western Ecuador in which Buarremon brunneinuchus is unknown. The latter, however, is found in this zone in western Ecuador both to the north and to the south of the region inhabited by inornatus.
- 2.—The two birds appear to agree in general habits and choice of haunts.
- 3.—In nestling plumage Buarremon inornatus resembles B. brunneinuchus.
- 4.—Adult Buarremon inornatus differs from adult B. brunneinuchus in the greater expanse of white in the underparts and in lacking a black pectoral band, but individuals occur in which the white area below is of even less extent than in brunneinuchus and which show traces of a pectoral band.
- Fig. 2. Map illustrating the known distribution of Buarremon brunneinuchus and B. inornatus in the Subtropical Zone of Ecuador. (See opposite page.)

Black dots () localities at which B. brunneinuchus has been taken. Note that it occurs in the Western as well as the Eastern Andes, and that it is found both to the north and to the south of the range of inornatus.

Circles (O) localities at which B. inornatus has been taken. Note that inornatus is confined to the Chimbo Valley drainage and that this valley is partly isolated by the main Andean system on the east and the Chillanes range (reaching to the Temperate Zone) on the west.

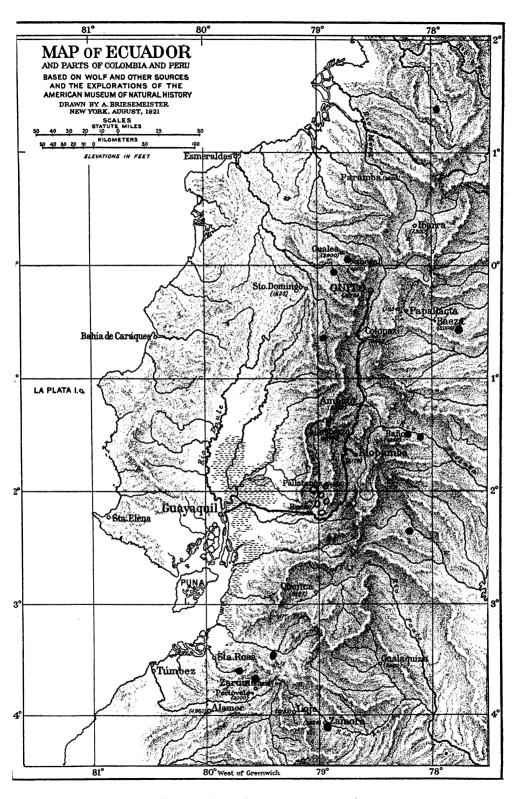


Fig. 2. (For explanation see page 254.)

Conclusions

The facts above presented appear to warrant the following conclusions.

- 1.—That Buarremon inornatus is a representative of Buarremon brunneinuchus.
- 2.—That the variations in pattern and color occurring in the underparts of *B. brunneinuchus*, throughout the range of that species, are individual and are not due to age, sex, season, climatic, or other observable environmental factors.
- 3.—That there is an inherent tendency in B. brunneinuchus toward the restriction of the grayish colors of the underparts and the disappearance of the black pectoral band.
- 4.—That isolation, partial or complete, has alone supplied the necessary environmental conditions for the perpetuation of these variations as the specific attributes of *Buarremon inornatus*.

The Relationships of Buarremon brunneinuchus to Pipilo torquatus

Pipilo torquatus inhabits the Temperate Zone at the southern end of the Mexican tableland. I have taken it at Las Vigas (8000 ft.) in Vera Cruz, immediately above Jalapa (4000 ft.) in the Subtropical Zone, where I found Buarremon brunneinuchus. The experience impresses me with the probability that one bird is the zonal representative of the other.

In general appearance torquatus closely resembles brunneinuchus, but it is a somewhat larger bird with a shorter, stouter bill, heavier feet and less rounded wing, differences which we associate with increase in activity incident to life in a colder region of more open growth.

In color the two birds are strikingly alike, but torquatus has more black and less chestnut on the head, the pectoral band is wider, the wings and tail greener, the flanks and crissum browner; in some individuals there are broken blackish malar streaks, the orange-rufous post-ocular stripe is wanting, but there is usually a broad, white, black-streaked superciliary reaching from the base of the bill to the nape.

The replacement of the orange-rufous post-ocular by a white and black superciliary is the most positive character separating the two birds. It is, however, a very variable character and in one of our specimens of the western race of torquatus (alticola) is represented only by the small white supra-loral spot which is also present in brunneinuchus. Another specimen from the same locality (Pisagua, Jalisco) has the superciliary fairly well developed on one side but almost absent on the other, while in our five remaining Jalisco specimens it is present in a variable degree.

We shall find later, in our study of the Buarremon assimilis group, that the superciliary is an important, though small, diagnostic mark, distinguishing one form from another but, in this group, also, subject to much variation in individuals from the same locality. While, therefore, we may believe that those differences in size of bill and feet, and in shape of wing which separate Pipilo torquatus from Buarremon brunneinuchus are the effects of environment acting through habit, and, while those differences of degree which distinguish them in color may also be due to the influence of external causes, the presence of a superciliary, I am convinced, both in this instance and in others to be described beyond, is to be attributed to mutation.

The Geographical Origin of Buarremon brunneinuchus

While this paper is not designed to be a study in distribution, geographical and physical origin are such closely related subjects that one cannot be discussed satisfactorily when the other is excluded. In this connection, for example, it is important for us to consider whether Buarremon brunneinuchus is derived from Pipilo torquatus or the reverse.

Species occupying the upper life zones in more or less isolated mountain areas are, as a rule, the descendants of forms occupying lower zones. Under the application of this law *Pipilo torquatus* should be derived from *Buarremon brunneinuchus*. The region occupied by *torquatus*, however, cannot be regarded as a more or less isolated mountain zone but rather as a portion of a vast tableland extending northward into the United States, the life of which has been received from the north rather than from the comparatively restricted region lying below it.

Subtropical forms of probable Temperate Zone origin are rare. Probably *Hesperiphona abeillæi* may be so considered and, in my opinion, *Buarremon brunneinuchus* also belongs in this small class.

The fact that in Vera Cruz and nowhere else throughout its range of 5000 miles or more *Buarremon brunneinuchus* has a Temperate Zone representative inevitably leads to the conclusion that the bird has existed longer in Vera Cruz than in any other part of its range.

Whatever may be its physical origin, we may then accept Vera Cruz as the probable region of its geographical origin. From this point it has extended its range southward throughout the Subtropical Zone almost to Bolivia, but in no place has it entered the Temperate Zone.

On the other hand, *Pipilo torquatus* exhibits characters which indicate that it is an older species than *brunneinuchus*. It includes two forms, and, through *Pipilo nigrescens*, bears relationships to *Pipilo*

macronux which definitely connect it with the great pipiline group. Furthermore, its juvenal plumage emphasizes its affinities with Pipilo. There are, indeed, greater differences between Pipilo torquatus and Buarremon brunneinuchus in juvenal than in adult plumage, a fact for which I am unable to suggest an explanation, though it evidently indicates that the two birds have been separated for a long period.

This brief survey of the relationships of *Pipilo torquatus* and *Buar*remon brunneinuchus leads to the conclusion that the latter is derived from the former, and that the characters separating them are attributable in part to the influence of environment in part to mutation.

THE SECOND GROUP

The fact that species of the two major groups into which, for convenience, we have divided the members of the genus Buarremon are in some instances found associated, together with the differences in color presented by their juvenal plumages, indicates that they represent two distinct branches of the genus.

This second group not only contains a larger number of species than the first, but the evolutionary factors apparently responsible for its differentiations are more numerous and include not only individual variations or mutations, but changes in zonal distribution which present marked differences in environment. There are also present abrupt variations as well as those variations of degree which distinguish what are commonly termed geographical races and which, whatever their origin, do not sharply set one form off from another but connect them so gradually by intergradation through a comparatively wide area that it is impossible to draw a line definitely demarking the range of one form from that of its one or more racial representatives.

As in the First Group, the instance of apparent mutation to which I now wish especially to call attention affects the pectoral band. There are, however, other, though minor, variations to be considered, and all are so closely related and seem to possess so direct a bearing on certain problems of discontinuous distribution in the genus Buarremon that it seems essential to review, at least briefly, all the forms of the group.

Fig. 3. Distribution of the gray and black or black-crowned members of the genus Buarremon. Note that the areas occupied by species without a breast-band are white, those with a breast-band, black; also discontinuity in the ranges of whitebreasted and breast-banded species. (See opposite page.)

- 1. Buarremon virenticeps.
- 2. Buarremon assimilis costaricensis.
 3. Buarremon atricapillus tacarcunæ.
 4. Buarremon basilicus.
- 5. Buarremon phaopleurus.
- Buarremon phygas.
 Buarremon assimilis assimilis.
- 8. Buarremon assimilis nigrifrons.
- 9. Buarremon poliophrys.
- 10. Buarremon torquatus.11. Buarremon fimbriatus.12. Buarremon borelli.

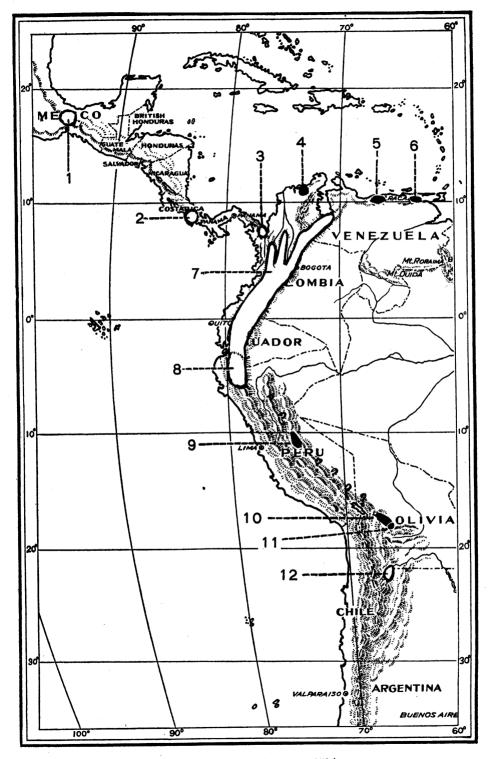


Fig. 3. (For explanation see p. 258.)

SECOND GROUP; SECTION A. (PECTORAL BAND ABSENT)

The species of the black or black and gray-crowned members of the genus *Buarremon* having white underparts with no pectoral band have a singular distribution (see map).

Buarremon assimilis, the most widely distributed form, occupies the Temperate Zone of Colombia and northern Ecuador, the Subtropical Zone of southern Ecuador (where it is represented by the intergrading form B. a. nigrifrons), and the Subtropical Zone of southwestern Costa Rica (where it is represented by the intergrading (?) form B. a. costaricensis). A distinct white-breasted species (B. virenticeps) is restricted to the highlands of southern Mexico, and, after passing in Peru and Bolivia three species with a black breast-band, another white-breasted species (B. borelli) is found in northern Argentina.

At the northern end of the Central Andes of Colombia, immediately below the range of assimilis in the Temperate Zone, a white-breasted species with a wholly black head (B. atricapillus) occupies the Subtropical Zone, and in the same zone of the mountains of eastern Panama this bird is represented by a race, B. atricapillus tacarcunæ.

While it is evident that we have here exceedingly interesting problems in distribution and the origin of zonal forms, it seems wise not to pursue this phase of the subject any farther than need be, but to focus our attention on the question of mutation with which we are here especially concerned. Our interest in this connection centers, therefore, on Buarremon assimilis, for it is in the heart of the range of this species that the evidence to be considered has been found.

Buarremon assimilis

Buarremon assimilis assimilis (Boissonneau) Buarremon assimilis nigrifrons Chapman Buarremon assimilis costaricensis Bangs

DISTRIBUTION.—In the Mérida region of western Venezuela,¹ in all three ranges of the Colombian Andes (but not in the Santa Marta group), and southward to northern Ecuador, this species is found in the humid Temperate Zone, that is, between the elevations of, approximately, 9000 and 12,000 feet. In southern Ecuador, however, it occupies the Subtropical Zone. Only one of our thirty-nine specimens from southern Ecuador was taken above an altitude of 7000 feet and the greater number were taken between 2500 and 5000 feet. If all of these specimens were from the Western Andes, we might attribute the lower altitude of their

¹I have seen no Venezuela specimens.

range to the effects of the Humboldt Current, which markedly lowers the height of zonal boundaries in those portions of western Ecuador to which its influence extends, but since some of our specimens come from as far east as Loja, it is evident that this cool littoral current is not the sole factor which has created the difference in the zonal distribution of this species in Ecuador. But, whatever be the cause, the result is to create a pronounced difference in the climatic environment of the birds of northern and southern Ecuador.

Buarremon assimilis belongs in that large group of species which, living above the Tropical Zone in Colombia, are wanting in Panama (except, in some instances, the higher elevations of eastern and western Panama) but appear again in Costa Rica. There, as in southern Ecuador, it is found in the Subtropical Zone, and consequently exists under different environmental conditions from those which prevail in the range of those members of the species which inhabit the Temperate Zone.

Habits.—In general habits Buarremon assimilis resembles B. brunneinuchus. Its home is in the dense undergrowth, whether of the humid Temperate or Tropical Zone. It is by no means shy and this fact, in connection with its comparative abundance, makes it an easy bird to secure. Like brunneinuchus, it is a silent bird and I have never knowingly heard it either call or sing.

The eggs, according to Stolzmann (Proc. Zoöl. Soc., London, 1880, p. 196), are uniform pale greenish.

Characters of the Adult.—If one should remove the chestnut cap from *Buarremon inornatus* and give it a black one with more or less gray through the center, at the sides of the neck as well as crown, he would have, essentially, a duplicate of *B. assimilis*. In other words, assimilis is a bird with an olive-green back and (externally) wings; a blackish tail; yellow wing-edge; snowy white underparts, with grayish or olive grayish sides; black head and cheeks, with gray markings of variable extent. These variations will be described later.

Variations with Age.—The juvenal (nestling) plumage, judging from a specimen in the post-juvenal molt, is uniform dull olive-green above, streaked with yellowish below. The black areas in the crown of the adult are a very dark brown, while the adult's gray head-stripes are olive-green. Compared with the juvenal plumage of *B. brunneinuchus*, well-marked differences are noted. The latter is much darker, and less streaked below, and the chestnut cap with its orange-ochraceous border is suggested. These differences serve to emphasize the distinctness of the brunneinuchus and assimilis groups.

As the post-juvenal molt progresses, black feathers appear and the black crown areas are all well developed before gray replaces the green median and post-ocular stripes. At this stage there is a marked and possibly significant resemblance to the adult of *B. virenticeps* of the southern end of the Mexican tableland.

The plumage acquired by the post-juvenal molt, as with *B. brunnei-nuchus*, resembles that of the adult.

Sexual Variation.—The sexes are alike in color but, as in *B. brunneinuchus*, which, it will be observed, this species closely resembles in size and proportions, the male averages larger. The appended measurements were made from specimens taken in the Central and Western Andes of Colombia:

	Wing	TAIL	Tarsus
5 males	84-87.5	85-92	31-32
5 females	80-83	78-85	27-31

SEASONAL VARIATION.—Specimens from Ecuador representing eight months of the year show no seasonal variation in color, the effects of neither wear nor fading being noticeable.

Variation.—Prior to my study of this group of birds, I should have had no hesitation in labeling as "geographic" certain variations presented by *Buarremon assimilis*. Now I frankly confess I do not know whether to attribute them to the direct action of environment or to the influence of isolation in preserving slight variations produced by internal or germinal, rather than external or environmental, factors.

It is important to remember, however, that both of the slightly differentiated races of assimilis of the Temperate Zone inhabit another zone—the Subtropical—and hence are afforded both a different environment and isolation. At the best, the characters separating all three races are slight, and affect chiefly the pattern of coloration of the head. They may be summarized as follows:

Characters of the Races of Buarremon assimilis

Buarremon assimilis assimilis. (Temperate Zone, Colombia and Northern Ecuador.)

Sides of crown and cheeks black; gray median stripe extending from the bill to the nape, sometimes (about one bird in three) distinctly white at the base of the bill; supra-loral stripe distinctly white, not reaching to the bill; post-ocular region gray, broad, widely separating the black aural region from the black crown-stripe.

Buarremon assimilis nigrifrons. (Subtropical Zone, Southern Ecuador and Northern Peru.)

Black of sides of crown and cheeks more extensive, gray median stripe narrower usually not reaching in front of eyes; white line at base of bill usually present (about 90 per cent of specimens examined); supra-loral stripe distinctly white and reaching almost, if not quite, to the base of the bill; post-ocular region gray, narrow, sometimes blackish and then not definitely separating the black aural region from the black crown-stripe.

Buarremon assimilis costaricensis. (Subtropical Zone, Southwestern Costa Rica.)

Black of sides of the crown and cheeks much as in assimilis assimilis; gray median stripe reaching to the bill; white line at base of bill usually absent; supra-loral stripe GRAY, not reaching base of bill; post-ocular region as in assimilis assimilis.

Variations in Size

	WING	T AIL	1 ARSUS
$B.\ a.\ assimilis^1$	84.0-87.5 (86.0)	85.0-92.0 (87.0)	31.0-32.0 (31.2)
B. a. nigrifrons,2	79.0-89.5 (83.0)	75.0-87.0 (80.0)	28.0-30.2 (29.3)
B. a. costaricensis,3	81.0-86.0 (84.0)	76.0-81.0 (78.6)	27.0-28.0 (27.7)
		Culmen	
		LENGTH	\mathbf{Depth}
B. a. assimilis ¹		17.0	7.1-7.5 (7.2)
B. a. nigrifrons, ²		17.3-19.0 (18.3)	7.7-8.0(7.4)
B. a. costaricensis. ³		18.0-19.0 (18.3)	8.3 - 8.5(8.4)

It will be seen that most of the variations in color are not constant. Thus, in all three races specimens from the same place may or may not have a white line on the forehead at the base of the bill, while in two of them the white supra-loral stripe may or may not reach the bill; and in one the gray median line may or may not reach the forehead. In other words, there is sufficient individual variation in specimens from the same locality to bridge their average differences.

Whether variations of this character may be attributed to the action of environment or to an inherent tendency to vary is open to argument. In my belief it is difficult to associate them with the climatic causes we find so potent among song sparrows (*Melospiza*) for example, nor can one

¹West Colombia.

²Alamor, southwest Ecuador. ³Boruca, southwest Costa Rica.

understand how a climatic environment may affect only certain individuals at a given locality while producing no effect on others.

In size, as in color, it will be seen that, while there are average differences in the length of wing, tail, tarsus, and bill, they are all practically covered by the range of individual variation in only five specimens of each race, but in depth of bill the three specimens of the Costa Rican bird are different from the remaining two forms.

Postmortem Variation in Color.—As with Buarremon brunneinuchus, skins of B. assimilis changed perceptibly with age. "Bogotá" and "Quito" specimens collected probably between 1860 and 1875, when compared with others taken in 1922, have the upperparts much more yellow (approximately the difference between citrine and dark olive-citrine), the tail and wing-quills (except the outer margins) dark sepia (instead of black), the flanks browner.

The differences in color originally attributed to B. a. costaricensis were evidently in part due to the use of old "Bogotá" skins in comparison.

Individual Variation.—Conscious of the impossibility of drawing a sharp distinguishing line between individual and geographic variations, I pass over here those characters of the crown to which attention has been called and which, whatever be their cause, may be connected with locality, and come at once to the instance which first attracted my attention to the possibility of mutation in this group.

Buarremon assimilis, a white-breasted bird, ranges southward to southern Ecuador and the adjoining parts of Peru. But some 300 miles farther south (Maraynioc, Central Peru) it is represented in the Temperate Zone by a bird (Buarremon poliophrys) which is exactly like it in color but has a pronounced black pectoral band. In other words, the differences between B. assimilis and B. poliophrys are just the same as those that distinguish B. inornatus from B. brunneinuchus. It should be added that in its head markings poliophrys resembles true assimilis, not assimilis nigrifrons. That is, the median gray crown-stripe reaches the bill and, in the single specimen I have, the supra-loral stripe does not. In size this bird resembles nigrifrons but has a shorter culmen (15.5 mm.).

Most ornithologists have accepted differences of this kind as inexplicable under existing conditions or as possibly the cumulative effects of geographic variations; but, as in the case of *B. brunneinuchus* and *B. inornatus*, specimens recently acquired by our museum lead me to believe that they may be due to mutation. The most interesting of these specimens was acquired in August, 1922, from Mr. Ludovic Söderstrom in Quito. While examining Mr. Söderstrom's collection of birds I found

numbers of specimens of Buarremon assimilis assimilis which, like those contained in our own collection, were wholly normal, white-breasted birds, but among them was one with a COMPLETE BLACK BREAST-BAND! The bill agrees with that of assimilis but, so far as color is concerned, the bird is essentially B. poliophrys of Central Peru.

This specimen (No. 173,089, Amer. Mus. Nat. Hist.) was taken at Nono in the Temperate Zone some fifteen miles northwest of Quito. Normal specimens of assimilis were also taken at the same locality. We have one in our collections; while at Verdecocha, about seven miles from Nono, and at approximately the same altitude (9400 ft.), we collected four specimens of true assimilis.

It might be suggested that this specimen with the black pectoral band was in truth an individual of the Peruvian *poliophrys* which had wandered far from its own home. But, aside from the fact that in measurements, particularly the size of the bill, the Nono specimen agrees with *assimilis assimilis*, I find that it is not the only specimen in our collections showing the pectoral band which distinguishes *poliophrys* from *assimilis*.

A second specimen was taken by A. A. Allen at Laguneta in the Temperate Zone near the northern end of the Central Andes of Colombia, remote, therefore, from the range of *poliophrys*. In it the pectoral crescent is not complete but is a necklace rather than a band. It is, however, sufficiently developed to be, when considered in connection with the Nono bird, an exceptionally significant variant.

Buarremon atricapillus

Buarremon atricapillus atricapillus Lawrence. Buarremon atricapillus tacarcunæ Chapman.

DISTRIBUTION.—Buarremon atricapillus atricapillus is known definitely only from the Subtropical Zone at the northern end of the Central Andes in Colombia, but it may occur also in both the Eastern and Western Andes. Its close relative, B. atricapillus tacarcunæ, has been found only in the Subtropical Zone of eastern Panama.

Characters and Variations.—The Colombian form, true atricapillus, resembles B. assimilis but has the top and sides of the head and nape solid black without median or superciliary stripes, but in one of our four specimens there is, on one side, a trace of a white supra-loral stripe at the base of the bill. The latter member is thicker than in assimilis and the culmen is more decurved.

While assimilis is presumably a zonal representative of atricapillus, the fact that they apparently do not intergrade, though occupying ad-

joining ranges in the same mountain range, indicates their specific distinctness.

Buarremon atricapillus tacarcunæ of eastern Panama is more deeply colored above than true atricapillus; it has the heavy bill of that form but the head, instead of being black, has gray median and post-ocular stripes as in B. assimilis nigrifrons. Three of our four specimens are wholly without a supra-loral stripe. The fourth shows a trace of one, and this specimen, with one other, has a white mark on the forehead at the base of the bill.

If the ranges of atricapillus and tacarcunæ were reversed, we might well imagine that the latter was a true geographic intermediate between assimilis and atricapillus, but, as has just been said, the specific distinctness of these two forms is apparently proved by their occupation of adjoining zones without intergrading. We thus have a related but distinct species occupying an area between that of two races of B. assimilis (assimilis assimilis and assimilis costaricensis), a phenomenon I am wholly unable to explain.

Buarremon virenticeps Bonaparte

DISTRIBUTION.—"Southern Mexico in States of Jalisco (San Sebastian), Michoacan (Patzcuaro), Morelos (Huitzilac), Puebla (La Puebla), Mexico (Amecameca, City of Mexico, etc.), and Guanajuato" (Ridgway).

This distant outlier of the assimilis group is restricted to the southern end of the Mexican tableland. From between this region and Costa Rica no member of the group has been recorded.

Buarremon virenticeps resembles assimilis in general coloration. The supra-loral stripes and mark on the forehead at the base of the bill are white, but the post-ocular stripe is greenish yellow, the median stripe is gray anteriorly and yellowish posteriorly, and the breast is more or less grayish. Although obviously distinct, this species appears to be a representative of assimilis and the probability of their close relationships is emphasized by the resemblance between virenticeps and the juvenal plumage of assimilis.

Buarremon borelli Salvadori

DISTRIBUTION.—Known only from San Lorenzo, Province of Jujuy, northern Argentina.

Characters.—This species, the only member of the genus of which I have seen no specimens, is described as resembling *Buarremon assimilis*, but differing from that species by possessing a conspicuous white super-

ciliary stripe. In the latter character it therefore resembles *B. fimbriatus* of Bolivia, and the fact that in that species the breast-band shows a tendency to disappear suggests that *borelli* may be a mutant, bandless form of *fimbriatus*, just as we believe *inornatus* is of *brunneinuchus*.

SUMMARY

- 1.—The white-breasted, black or black and gray-crowned members of the genus *Buarremon* are distributed discontinuously from southern Mexico to northern Argentina. Species having a pectoral band separate the ranges of those without it.
- 2.—So far as is known, these birds are sedentary inhabitants of undergrowth and in habits resemble B. brunneinuchus and B. inornatus. The fact that a representative of this group (B. assimilis nigrifrons) is found associated with B. brunneinuchus, in connection with the marked differences shown by the juvenal plumages of brunneinuchus and assimilis, indicates that they belong to distinct branches of the genus.
- 3.—Buarremon assimilis, the most widely distributed species of the group, is composed of three races of which (1) B. assimilis assimilis occupies the humid Temperate Zone of western Venezuela, Colombia (except Sta. Marta) and northern Ecuador; (2) B. assimilis nigrifrons the Subtropical Zone of southern Ecuador and northern Peru; and (3) B. assimilis costaricensis the Subtropical Zone of southwestern Costa Rica, between which region and Colombia the species is unknown.
- 4.—These forms are differentiated from one another by average differences in the markings of the head and in size, but, with some exceptions, the markings which characterize one race are occasionally exhibited by individuals of one or both of the other races, and, with the exception of the depth of the bill in the Costa Rica race, the average differences in size are bridged by variation among individuals from the same locality.
 - 5.—There is essentially no variation in color with sex or season.
- 6.—Old museum specimens apparently differ in color from recently collected ones.
- 7.—A pronounced and significant case of individual variation is shown by a specimen from northern Ecuador which, in possessing a fully developed black pectoral band, exactly resembles in color *Buarremon poliophrys* of Central Peru, while in a specimen from northern Colombia this band is partly developed. In measurements these specimens agree with *assimilis*.
- 8.—Buarremon atricapillus atricapillus inhabits the Subtropical Zone at the northern end of the Central Andes, where its range adjoins

- that of *B. assimilis assimilis*. It has a wholly black head and a stout bill, and is evidently specifically distinct from *assimilis*. One specimen out of four examined has a trace of a white supra-loral stripe on one side.
- 9.—In the Subtropical Zone of eastern Panama atricapillus is represented by a race (tacarcunæ) with a more deeply colored back and gray head-stripes (much as in B. assimilis nigrifrons). The supra-loral stripe is absent except in one of four specimens examined, and this, with one other, has a white line on the forehead.
- 10.—Buarremon virenticeps, of the southern end of the Mexican tableland, is a distinct species with the head-stripes posteriorly yellowish, a character to some extent shown in the juvenal plumage of assimilis.
- 11.—Buarremon borelli, of northern Argentina, the most southern member of the genus, resembles B. assimilis but has a white superciliary as in B. fimbriatus.

Conclusions

Various theories may be presented to explain the distribution of the species of the genus *Buarremon* which are contained in the group we have just considered. I will, however, reserve what I have to say on this subject for a general summing up of the evidence presented by a study of all the species of the genus and confine myself there to a consideration of the variations which we have found to occur in this group of black or black and gray-crowned birds with white breasts having no pectoral band.

- 1.—While the variations in the color and pattern of head markings in *Buarremon assimilis* are correlated to a large extent with geographic distribution, local variation in them is so great that the markings which characterize one race are often exhibited by one or both of the other races, suggesting that their occurrence is due to an inherent tendency to vary rather than to the direct action of environment.
- 2.—These variations may, therefore, be considered as slight mutations which, when they occur in a sufficient number of individuals under favorable environmental conditions, become prevalent and characteristic.
- 3.—The change from the Temperate to the Subtropical Zone in Ecuador and the gap in the range of the species between Costa Rica and Colombia have supplied the isolation from the main range of the species needed for the perpetuation of the differentiating characters exhibited by the southern Ecuador and Costa Rican forms.
- 4.—The appearance in the heart of the range of Buarremon assimilis of an individual of that species possessing a fully developed pectoral

band is an instance of pronounced mutation which demonstrates a potentiality for abrupt variation independent of environment.

- 5.—The fact that, so far as color is concerned, the acquisition of this band practically changed an individual of *Buarremon assimilis* from northern Ecuador into an individual of *Buarremon poliophrys* of Central Peru, suggests that the latter species is a mutant of the former.
- 6.—The increase in intensity of color shown by all our specimens of Buarremon atricapillus tacarcunæ, of eastern Panama, may well be due to the greater humidity of its range as compared with that of B. atricapillus atricapillus of Colombia; but the appearance in the first-named form of gray head-stripes, and in certain individuals of both forms of white supra-loral stripes, is believed to be due to germinal, rather than environmental, influences.
- 7.—Buarremon borelli of northern Argentina is believed to be a representative of B. fimbriatus of Bolivia which, as in the case of B. inornatus, has by mutation lost its pectoral band.

SECOND GROUP; SECTION B. (PECTORAL BAND PRESENT)

Reference to the map will show how widely separated are the ranges of the black and gray-crowned species of *Buarremon* which have a pectoral band.

Thus, B. basilicus is confined to the Subtropical Zone of the Santa Marta mountains of northern Colombia, B. phæopleurus occupies this zone in the Caracas region, B. phygas is found in the mountains of northeastern Venezuela, B. poliophrys the humid Temperate Zone of east Central Peru, B. torquatus, the Subtropical Zone of the east Andean slopes at Bolivia, and B. fimbriatus is known from a single locality in the last-named region.

Further collecting will doubtless considerably extend the known ranges of certain of these species, especially that of *B. poliophrys*, but it is possible that only the ranges of *B. torquatus* and *B. fimbriatus* may adjoin each other.

While these forms bear a general resemblance to one another so close that, if their ranges were continuous, they would probably intergrade, nevertheless, with the possible exception of *fimbriatus* and *phygas*, the characters separating them are sufficiently pronounced to prevent intergradation by individual variation and, taxonomically, therefore, they may rank as "species."

The two exceptions named as possibly intergrading by individual variation more closely resemble one another than do any other birds in the section; nevertheless, one is found in Bolivia the other in north-eastern Venezuela!

From an evolutionary point of view, our specimens of the two Bolivian forms are the most instructive, one of them furnishing an apparent case of the combined effects of mutation and isolation.

Before presenting the evidence on which this assumption rests, we may review briefly the remaining members of this section, beginning at the north.

Buarremon basilicus Bangs

DISTRIBUTION.—Subtropical Zone, Santa Marta Mountains, Colombia.

Characters.—Back and wings (externally) browner than in any other member of the genus, between olive-citrine and medal-bronze, rather than olive-green; tail and wings brownish fuscous without olivaceous; median crown-stripe gray, reaching to base of bill; superciliary stripe gray, whiter anteriorly (supra-loral stripe) and reaching to base of bill; sides of the breast gray but flanks and under tail-coverts decidedly brownish; bill long as in *phæopleurus*.

Variations.—Nine specimens taken from March to June are exceedingly uniform in color, pattern, and size. In one example the central crown-stripe is appreciably whiter at the base of the bill but aside from this the series presents practically no variation.

Doubtless largely because of its practically insular isolation, *Buar-remon basilicus* is the most highly differentiated member of this section of the genus.

Buarremon phæopleurus Sclater

DISTRIBUTION.—Subtropical Zone of the Caracas region, Venezuela. Characters.—Back, wings, and tail, olive-green yellower than the other forms of the section; central crown-stripe gray; superciliary stripe snowy white, both reaching to or nearly to the base of the bill; flanks and lower tail-coverts yellowish or olivaceous old gold; bill large as in basilicus.

Variations.—I have but one specimen of this species and cannot therefore determine its variations. In its white superciliary stripe it resembles *B. phygas* of northeastern Venezuela, as well as *B. fimbriatus* of Bolivia, but it is yellower above than either and lacks the fringed breast-band of *fimbriatus*.

Buarremon phygas Berlepsch

DISTRIBUTION.—Mountains of northeastern Venezuela (Guacharo; Las Palmales).

Variations.—Back, wings, and tail olive-green, much as in *B. fimbriatus*; head markings also as in that race; the superciliary being white and reaching to the bill; breast-band nor fringed; bill, small. Of this species I have but one specimen, which, except for its black unfringed breast-band and possibly slightly yellower back, can be closely matched by examples of *B. fimbriatus* of Bolivia.

Buarremon poliophrys Berlepsch and Stolzmann

DISTRIBUTION.—Temperate Zone, east Central (and southern?)
Peru.

Characters.—Resembling B. assimilis assimilis but with a black breast-band and a smaller bill; superciliary gray but with a whitish tendency above the lores, not (?) reaching the bill; median stripe gray reaching the bill and whitish anteriorly; tail blackish.

Variations.—I have but one specimen of this species the relationships of which to *B. assimilis* have been commented upon under that species.

Buarremon torquatus (d'Orbigny and Lafresnaye)

DISTRIBUTION.—Subtropical Zone, Yungas region, Bolivia.

Characters.—Back olive-green as in *B. assimilis*; tail brownish black; central crown-stripe gray usually reaching nearly if not quite to the bill and usually whitish anteriorly; superciliary white, not reaching to the bill; breast-band, in some specimens, with a slight whitish margin; bill slightly smaller than in assimilis.

Variations.—Eleven specimens taken in May and June at Incachaca (7700 ft.) and Yungas (3600 ft.), department of Cochabamba, are very uniform in general color but present considerable individual variation in pattern. Thus, the median crown-stripe may be continuous or broken; it may or may not reach the bill and the forehead may be black, unmarked, or divided by white or whitish line; the superciliary extends sometimes half-way from the eye to the bill, at others does not quite reach to the anterior margin of the orbit. The black breast-band usually has at least traces of whitish margins, but in some species they are barely evident.

Buarremon fimbriatus Chapman

DISTRIBUTION.—Known only from Tujma (alt. 8200 ft.) "a ravine near Mizque," Dept. of Cochabamba, Bolivia.

CHARACTERS.—Resembling B. torquatus but back paler, tail olive-greenish as in B. phygas of northeastern Venezuela; superciliary stripe white, REACHING THE BASE OF BILL; breast-band conspicuously margined with white or whitish; flanks and under tail-coverts paler; wings and tail averaging longer, bill shorter.

Measurements

NAME	PLACE	Sex	Wing	TAIL	CULMEN
B, fimbriatus	Tujma, Bolivia	o ⁿ	85.0	83.0	16.0
"	u ú	♂	89.0	86.0	17.0
B. torquatus	Incachaca, Bolivia	♂	82.0	81.0	18.0
"		o ⁷	83.0	79.5	18.0
B. fimbriatus	Tujma, Bolivia	Q	79.0	78.0	16.5
"	" "	ç Q	79.5	81.0	15.5
B. torquatus	Incachaca, Bolivia	Q	77.0	75.0	17.0
"	" " "	Ŷ	77.0	71.0	17.0

Variations.—Aside from differences due to age, eight specimens taken at Tujma in September show little variation in the markings of the head, both central crown-stripe and superciliary reaching the base of the bill in every one of them. There is, however, much variation in the development of the breast-band; in one example it is incomplete, being lacking on the left side and appearing more as a series of disconnected black markings on the center of the breast. It seems probable that, except for the vestiges of the pectoral band, this specimen must closely resemble the white-breasted *B. borelli* of northern Argentina.

Unfortunately, I am not sufficiently familiar with the topographic relations of the ranges of torquatus and fimbriatus to state whether they are in actual contact or whether the "ravine," in which all our specimens of fimbriatus were collected, is cut off from the range of torquatus.

It seems evident, however, that fimbriatus, like Buarremon inornatus, is a highly localized form. While its generally paler coloration may be due to climatic conditions, the pattern presented by the superciliary and fringed breast-band appears to be mutational in character and so clearly to differentiate this form from torquatus that not one specimen in our series of nineteen suggests intergradation between the two.

SUMMARY

1.—The ranges of species of the genus *Buarremon* having a black and gray head and a breast-band are, with one possible exception, discontinuous. Between the ranges of the northern and southern species, forms without a breast-band occur.

- 2.—Although representative and closely related, none of the forms of this section is known to intergrade and, taxonomically, they therefore may rank as species.
- 3.—The species most nearly resembling each other are *phygas* of northeastern Venezuela and *fimbriatus* of Bolivia.
- 4.—Buarremon basilicus of the Santa Marta Mountains is the most strongly differentiated form of the black and gray-crowned group; it shows but little individual variation.
- 5.—Buarremon phæopleurus of the Caracas region and B. phygas of northeastern Venezuela are nearly related but are geographically isolated from each other and do not intergrade.
- 6.—Buarremon poliophrys of eastern Central Peru differs from B. assimilis assimilis only in possessing a breast-band and smaller bill and may be a mutant form of that species.
- 7.—Buarremon torquatus, of the Yungas region of Bolivia, has the blackish tail of assimilis, but the superciliary—which does not reach the bill—is white and the breast-band is more or less fringed.
- 8.—B. fimbriatus, though geographically very near, seems specifically distinct from torquatus, of which it may be a localized mutant. It has an olive-green tail, a fringed breast-band and the white superciliary reaches the eye.

Conclusions

- 1.—That, although differing from the members of Section A of Group II in possessing a black breast-band, the members of this section are nevertheless representatives of the members of that section.
- 2.—That the differences between the members of Section A and Section B are due to mutation.
- 3.—That the differences between the members of Section B are in part due to the direct action of environment, in part to mutation, both being made effective by isolation.

GENERAL REMARKS

The summaries and conclusions already presented leave little to add to what I have previously said, so far as the genus *Buarremon* is concerned. It remains, therefore, only to comment briefly on what I believe to be the bearings of the facts presented on the study of the evolution and distribution of birds. I intentionally avoid here any discussion of the possible action of natural selection in establishing the characters which distinguish the forms of the genus *Buarremon*. Believing, however, that the presence or absence of a pectoral band, vertical streak, or super-

ciliary line does not materially affect a species' chances of success or failure. I also believe that natural selection has played no part in their development.1

There are among birds certain types of markings affecting definite areas which are of such common occurrence that they have received distinctive names in descriptive ornithology. Thus, we have such familiar terms as superciliary stripe, orbital ring, nuchal band, wingbars, malar streak, pectoral band, etc. These marks occur in birds of widely separated groups, and their presence does not, therefore, necessarily indicate degree of relationship in the birds possessing them. The pectoral band or crescent, for example, is found in several plover, in woodpeckers (Colaptes), shore-larks, the meadowlark, finches (Rhunchophanes), swallows (Riparia), warblers (Compsothlypis, Wilsonia), and thrushes (Ixoreus), to mention only a few instances among North American birds.2

Hundreds of other cases might be cited, were it necessary, to illustrate the recurrence of these familiar types of markings among distantly related birds. It is evident, therefore, that, just as we find barred, streaked, or vermiculated feathers, throughout the Class Aves, so, independent of relationships, there also exist certain kinds of markings which affect not single feathers but definite areas. Doubtless there is as deep-seated a physiological reason for the existence of a superciliary stripe in birds as there is for an eye-brow in man, but how it or other recurrent markings came into existence we have vet to learn. This is a problem to which Dr. Witmer Stone³ has called attention, and toward the solution of which Dr. Glover M. Allen4 has made a notable contribution.

We are here, however, less concerned with their cause than with their existence in many and very different kinds of birds, of widely different habits, living under widely varying conditions. It is also a fact that these markings are subject to much individual variation and that they may appear sporadically. The white eye-ring and post-ocular stripe of the common murre (Uria troile "ringvia"), the more or less complete pectoral band found in certain individuals of the piping plover (Ægialitis meloda "circumcincta"), and the white post-ocular stripes in some in-

In other words, I consider these markings as representing the "trivial, superficial characters that have, so far as known, no survival value" to which Morgan refers in the paper already cited (Science Monthly, XVI, No. 3, 1923, p. 241.

*Compare also Morgan's remarks on the occurrence of the same mutation in different species

⁽loc. cit., p. 247).

\$1912, 'The Phylogenetic Value of Color Characters in Birds,' Journ. Acad. Nat. Sci., Phila., Ser. 2, XV, pp. 31–319.

*1914, 'Pattern Development in Mammals and Birds,' Amer. Nat., XLVIII, pp. 385–412; 467–484; 550–556. Also 1920, 'Pattern Development in Teal,' Auk, XXXVII, pp. 558–564.

dividuals of the blue-winged teal (Querquedula discors "albinucha") are such pronounced instances of this kind of variability that the variants have been described as new forms.

The blackish band which appears on the breast of some individuals of the northern parula warbler, the black crown, sometimes dotted with white, which occasionally is worn by female vellow-bellied sapsuckers.3 are further instances among many which might be cited of individual variations, or mutations, which, either because they are too infrequent or because the isolation needed for their perpetuation is lacking, have not become fixed.

The species of the genus Buarremon supply us with what I believe · to be an essentially similar kind of variation, but the mountainous region they inhabit, either through secluded subtropic valley or isolated temperate area, has afforded the environment essential to its perpetuation. Whatever may be the origin of the pectoral crescent in this genus, environment is not now believed to play any part in its presence or absence. It may have developed cumulatively through the preservation of small variations, due to an inherent, unexplained tendency to vary. It may have come into existence full-fledged, just as suddenly as, in the case of Buarremon inornatus, it has disappeared. However this may be, a study of our material convinces me of its mutational character, and, if this view should prove to be correct, it will afford a clue to the origin of many differences in pattern of coloration which serve to distinguish one species of bird from another.

Aside from expressing the combined effects of variability and isolation, the presence or absence of a pectoral band may have no faunal Hence, the occurrence of breast-banded Buarremons in Venezuela and Bolivia is to be attributed to parallelism rather than to any more or less direct faunal relation between these two regions.

By parallelism also I would explain the presence of a white-breasted species in northern Argentina and again in Ecuador and Colombia. Thus parallelism may account for many cases of apparent discontinuous distribution, and the faunalist must beware lest he interpret resemblances as relationships and give to them a significance they do not possess.

Less striking than the appearance or disappearance of the pectoral band in Buarremon, but no less important, are the variations in the crown, superciliary, and supra-loral stripes, and in the fringe on the

Cf. Kennard, 1919, Auk, XXXVI, p. 455; Arthur, 1920, Auk, XXXVII, p. 127; Allen, 1920, Auk, XXXVII, p. 558.

Cf. Miller, 1909, Auk, XXVI, p. 309.

Out of 104 females in the collections of the American Museum and Dr. J. Dwight, 9 have black (instead of red) crowns and of these 6 have the crown more or less spotted with white.

breast-crescent. The resemblance in crown-markings between Buarre-mon atricapillus tacarcunæ of eastern Panama and B. assimilis nigrifrons of southern Ecuador, and the possession of a similarly extended superciliary in B. fimbriatus of Bolivia and B. phygas of northeastern Venezuela, may be accepted as instances of parallelism founded on a common ancestry and expressed through an inherent tendency to vary along certain lines; while in the fringed breast-band of fimbriatus we find the consummation of a character hinted at in torquatus.

The uniformly deeper coloration of tacarcunæ of Panama, and basilicus of Santa Marta, or the paler hues of fimbriatus, from a ravine on the east Bolivian highlands, may be attributed to the direct action of the existing climatic environment, but it is difficult to see any direct relation between environment and the presence or absence of a pectoral band or superciliary stripe. In general tone of color all the forms of the genus present only slight, indeed almost negligible, variation, but, as has been shown, there is wide variation in the pectoral band and head markings among birds from the same locality. These variations, therefore, are individual, not geographic or racial, and consequently may be attributed to internal or germinal, rather than to external or environmental, influences.

Nor are variations manifested only in what may be termed the stereotyped or unit characters of pectoral band, or superciliary streak, etc. They may affect the markings of the individual feather and thus materially alter the pattern of coloration of certain parts of the birds' plumage while leaving the balance wholly unchanged.

For example, a goatsucker (Systellura ruficervix ruficervix) of the Temperate Zone from northern Peru to western Venezuela has numerous rounded ochraceous spots on the upperparts, while a representative of it which we have recently discovered in the Temperate Zone of eastern Peru has essentially similar marks but with black centers. This variation might be considered as due to some unknown environmental factor did we not find in our large series of true ruficervix a specimen from near Bogotá, Colombia, marked much like the Peruvian bird. Hence it seems most probable that this is an individual or mutational rather than a geographical variation.

To replace the latter term with the former may not advance our knowledge of the fundamental causes of evolution in birds. If, however, while confessing our ignorance of the underlying factors, we admit that variations great and small may arise independently of any observable, external cause, and that chiefly through isolation, partial or complete, these variations (or mutations) may prevail as specific or subspecific characters, I am convinced that in some cases, at least, we shall have a demonstrable explanation of the origin of the species distinguished by such characters.

LIST OF SPECIMEN'S EXAMINED

Buarremon brunneinuchus.

MEXICO: Jalapa, 4400 ft., 8.

NICARAGUA: San Rafael del Norte, 4200 ft., 8; Mombacho, 3600 ft., 3; Muy Muy, 1; Rio Tuma, 1; Rio Coco, 1; Ocotal, 1; Peña Blanca, 1; Chontales, 1; Matagalpa, 2200 ft., 6.

Costa Rica: Navarito, 4000 ft., 2; Aquinares, 4000 ft., 4; Bonilla, 2000 ft., 3; Agua Caliente, 4500 ft., 1.

Panama: Boquete, Chiriqui, 14; Tacarcuna, 4600 ft., 16.

COLOMBIA: Western Andes, San Antonio, 7; Las Lomitas, 1; La Florida, 2; Gallera, 2; Cerro Munchique, 2; Ricuarte, 2; Central Andes, above Palmyra, 6800 ft., 4; Salento, 7000 ft., 4; El Roble, 7200 ft., 1; Sta. Elena, 9000 ft., 2; El Eden, 8300 ft., 1; La Candela, 6500 ft., 3; Eastern Andes, Andalucia, 3000 ft., 4; Aguadita, above Fusugasugá, 6500 ft., 3; Buena Vista above Villavicencio, 2; Bogotá, 2.

VENEZUELA: Culata, 9000 ft., near Mérida, 3; Escorial, near Mérida, 8000 ft., 2. ECUADOR, WESTERN: Mindo, 4400 ft., 1; El Chiral, 5350 ft., 4; above Zaruma, 6000 ft., 2; Salvias, 6600 ft., 1. EASTERN: above Zamora, 2; Macas region, 3.

Peru: Utcuyacu, 4800 ft., 1; Chilpes, 7300 ft., 1; Tulumayo, 4000 ft., 1; Torontoy, 7800 ft., 3; San Miguel Bdg., 5000 ft., 1; Rio Inambari, 2200 ft., 1; Santo Domingo, 6000 ft., 2.

Buarremon inornatus.

ECUADOR: Pallatanga, 4200-5000 ft., 5; Junction Chimbo-Coco, 2800 ft., 2; Porvenir, 1; Junction Chanchan and Chiguancay Rivers, 2500 ft., 3; Pagma Forest, 6200 ft., 1; 7200 ft., 2; "Jima" (see antea), 1.

Buarremon assimilis assimilis.

ECUADOR: Pichincha, 4; Yanacocha, 11000 ft., n. w. slope Pichincha, 1; Verdacocha, n. w. slope Pichincha, 4; Nono, 1.

Colombia: Andes w. of Popayan, 10340 ft., 3; Laguneta, 6; Sta. Isabel, 1; El Piñon (above Fusugasugá), 1.

Buarremon assimilis nigrifrons.

Ecuador: Alamor, 4550 ft., 10; Guaniche, 3200 ft., s. e. of Alamor, 3; Guachanomá, 9050 ft., 1; Cebollal, 3100 ft., Pacific slope, w. of Alamor, 1; Las Piñas, 3600 ft., Alamor Mts., 2; La Puente, 2500 ft., w. of Sta. Rosa, 1; Punta Sta. Ana, Portovelo-Loja Trail, 4000 ft., 3; Loja, 2; Salvias, Zaruma-Zaguaro Trail, 6600 ft., 2; Portovelo, 2700 ft., 9; above Zaruma, 6000 ft., 5.

Peru: Palambla 6 %.

Buarremon assimilis costaricensis.

COSTA RICA: Boruca, 3.

Buarremon atricapillus atricapillus.

COLOMBIA: no locality, the type; La Frijolera, 5000 ft., Cen. Andes, 2; Mts. near Honda, 1.

Buarremon atricapillus tacarcunæ.

PANAMA: Tacarcuna, 4.

Buarremon poliophrys.

PERU: Maraynioc, 1 3.

Buarremon torquatus.

Bolivia: Yungas, 3600 ft., 2 σ ; Incachaca, 7700 ft., 6 σ , 3 \circ .

Buarremon fimbriatus.

Bolivia: Tujma, 8200 ft., 2 0, 5 9, 1?

Buarremon basilicus.

COLOMBIA: Santa Marta, Valparaiso, 6 3, 3 Q.

Buarremon phæopleurus.

VENEZUELA: Silla de Caracas, 1 3.

Buarremon phygas.

VENEZUELA: Guácharo, 1 Q.



PLATE XIV

Mutation in Buarremon brunneinuchus

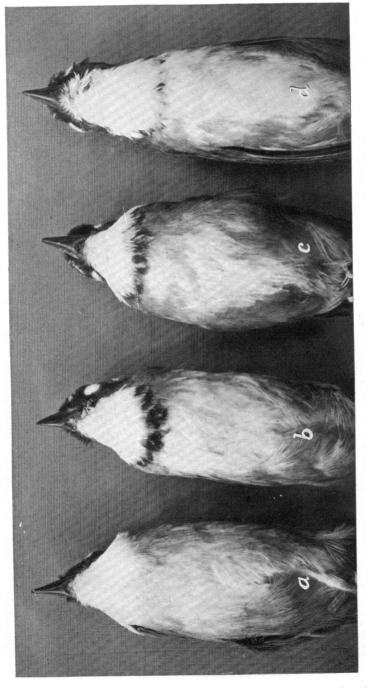
- $a.—Buarremon\ brunneinuchus,$ Amer. Mus. No. 122824; Buena Vista, above Villavicencio, Eastern Andes, Colombia.
- $b.\!-\!Buarremon\ inornatus,$ Amer. Mus. No. 173587; junction Rios Chimbo and Coco, Ecuador.
- c.—Buarremon brunneinuchus, Amer. Mus. No. 118183, Ricuarte, southwest Colombia. To show variability in pectoral band; an approach toward B. inornatus.
- d.—Buarremon inornatus, Amer. Mus. No. 173584; Los Llanos, near Pallatanga, Ecuador. To show indication of pectoral band.

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PLATE XV

Mutation in Buarremon assimilis

- $a.—Buarremon\ assimilis,$ Amer. Mus. No. 109376; Laguneta, Central Andes, Colombia.
 - b.—Buarremon poliophrys, Amer. Mus. No. 170069; Maraynioc, eastern Peru.
- c.—Buarremon assimilis, Amer. Mus. No. 173089; near Nono, Ecuador. Mutant specimen of B. assimilis with pectoral band of poliophrys.
- d.—Buarremon assimilis, Amer. Mus. No. 112857; Laguneta, Central Andes. Colombia. Showing indication of pectoral band.



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PLATE XVI

Mutation in Buarremon torquatus

- $a.—Buarremon\ torquatus,$ Amer. Mus. No. 138145; Incachaca, Cochabamba, Bolivia.
- b.—Buarremon fimbriatus, Amer. Mus. No. 139750; Tujma, Cochabamba, Bolivia. A mutant form of torquatus with fringed pectoral band, and superciliary reaching to the base of the bill.
- c.—Buarremon fimbriatus, Amer. Mus. No. 139756; Tujma, Cochabamba, Bolivia. Showing decrease in size of pectoral band, and consequent approach to B. borelli.

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PLATE XVII

Variations in the Superciliary a.—Pipilo torquatus torquatus. b.—Buarremon brunneinuchus. c.—Buarremon torquatus. d.—Buarremon fimbriatus

