Systematics and Geographic Variation in the Golden-breasted Puffleg *Eriocnemis mosquera* (Aves, Trochilidae)

ROBERT BLEIWEISS[1]

ABSTRACT

Analysis of geographic variation in five quantitative characters clarifies the systematics and distribution of the Andean hummingbird *Eriocnemis mosquera,* the Golden-breasted Puffleg. Birds of both sexes from the northern range limit of *E. mosquera* in the Central Cordillera of Colombia have bills that average 2 to 3 mm longer than in birds from southern Colombia and northern Ecuador. These longer-billed birds fit the diagnosis of *E. m. bogotensis* Hartert, a taxon described and known only from Bogotá trade skins. I conclude

that the population of longer-billed birds from the Central Cordillera was the likely source of Hartert's *E. m. bogotensis,* and that *E. mosquera* does not occur around Bogotá or anywhere else in the Eastern Cordillera of Colombia. Taxonomic recognition of the distinctive northern population is not warranted because male bill length varies clinally. *Eriocnemis mosquera* is but one of several species whose populations are differentiated within the Central Cordillera.

INTRODUCTION

The complex topography and ecology of the Andes has promoted evolutionary radiations in many bird families, especially hummingbirds. One obstacle to the complete description of evolutionary patterns in this large family is the many forms (especially subspecies) known only from trade skin specimens secured by native collectors during the 19th century. The intensive efforts made by native collectors around cities like Bogotá, Colombia and Quito, Ecuador, turned up many unusual and often unique specimens of potential biological importance. However, trade skins usually lack accompanying locality or other information. As a result, the geographic origin and taxonomic status of many forms

[1] Research Associate, Department of Ornithology, American Museum of Natural History; Honorary Fellow, Department of Zoology and Zoological Museum, University of Wisconsin, Madison, Wis. 53706.

known only from trade skins remain in doubt (Berlioz and Jouanin, 1944; Peters, 1945).

In the course of a study of speciation patterns in the principal polytypic hummingbird genera found in the Andes, I have had to investigate the biological significance of many forms known only from trade skins. *Eriocnemis* is among the most diverse and widespread of endemic Andean genera, and a number of problematic *Eriocnemis* taxa have been described. *Eriocnemis mosquera* is usually considered to be monotypic (Peters, 1945). However, Hartert (1897) described the subspecies *E. m. bogotensis,* which he distinguished from the nominate form by a longer bill (a difference of 2 to 3 mm). As the name indicates, the description was based upon Bogotá trade skin material. Unfortunately, the skins have no precise collecting locality information. This form was not recognized by Chapman (1917) who stated that he could detect no racial differences between an essentially topotypical specimen of *E. mosquera* and several Bogotá trade skins. Peters (1945) did not accept this subspecies, but Berlioz and Jouanin (1944) and Meyer de Schauensee (1948) suggested that more material was needed to evaluate variation within the species.

In this paper, I examine geographic variation in the bill and other quantitative characters in *E. mosquera,* and evaluate the evolutionary significance of the Bogotá specimens described by Hartert. The results of my study indicate a distinctive pattern of geographic variation in bill length that reinforces general biogeographic and evolutionary patterns among birds in the northern Andes.

MATERIALS AND METHODS

I examined all available study skins of *E. mosquera* from the ten museum collections cited in the Acknowledgments. I did not examine the holotype of *E. m. bogotensis* (in the British Museum, Natural History, Tring). In his description, Hartert (1897) mentioned only a difference in bill length between the nominate form and *E. m. bogotensis*; he did not discuss how or even whether he measured the bill or other characters. For each specimen I measured five mensural characters to the nearest 0.1 mm with dial calipers, including two different measures of bill length: (1) exposed culmen (EC), (2) culmen from flange of nasal operculum (CF), (3) chord of outer primary (P), (4) chord of wing from butt (WB), and (5) outer tail feather (OT) (Baldwin et al., 1931).

I distinguished immatures by their bill corrugations, which are absent in adults (Ortiz-Crespo, 1972; Bleiweiss, 1985). Sexing specimens was more problematic. Gonad data were provided on the labels of only two adult female specimens. However, the sex had been noted by the collector on the labels of all 42 adult specimens I examined. I followed the collectors' evaluations because most of the specimens (31 of 42 specimens, or 74%) were collected by M. A. Carriker, Jr. or members of F. M. Chapman's expeditions, who sexed their material by inspecting the gonads. In hummingbirds, the sexes are frequently dimorphic in size. The measurements of females without gonad data (13 of 15) were similar to the measurements of the two females with gonad data. This suggests that the collectors or preparators correctly identified the sex of these specimens.
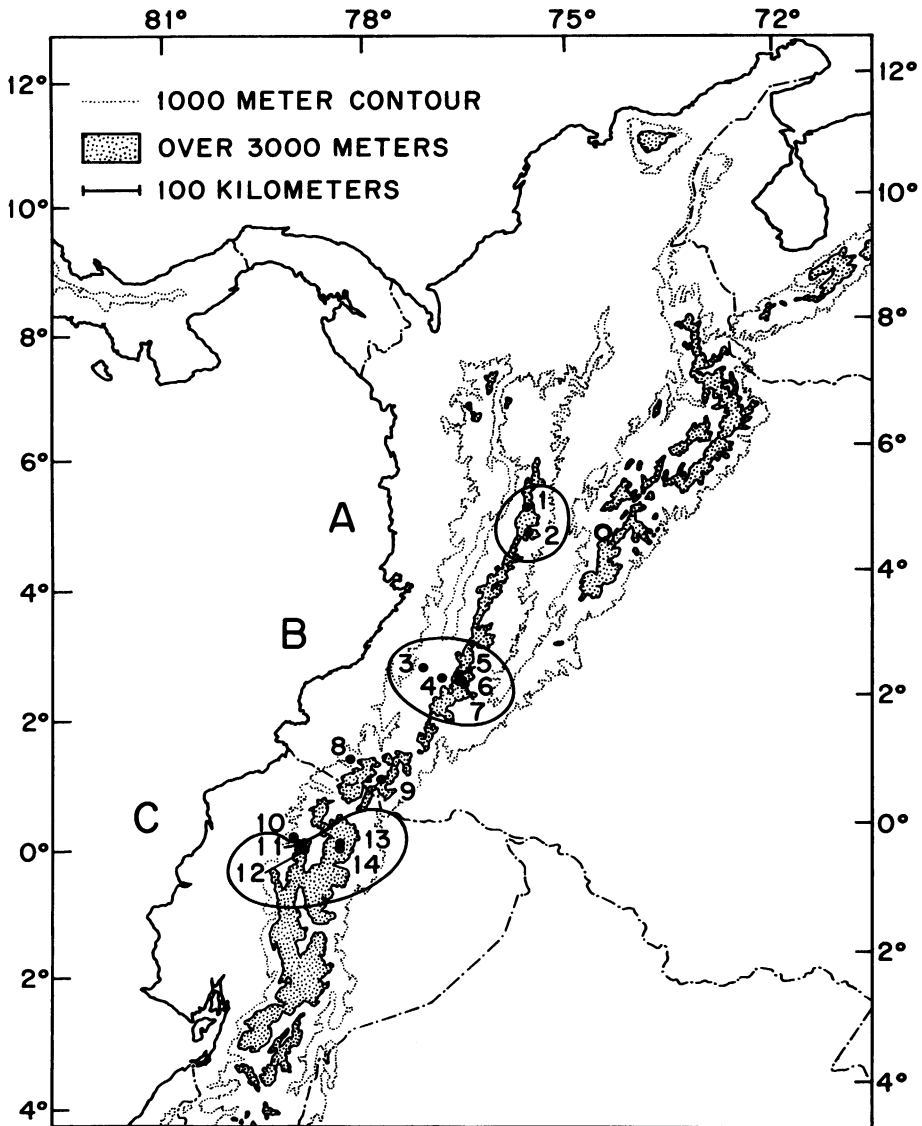
Fig. 1. Map of localities of specimens examined. *Colombia:* **A:** 1 = La Leonera, 2 = Santa Isabel; **B:** 3 = Coast Range west of Popayán, 4 = El Crucero (Cauca), 5 = Páramo de San Raphael, 6 = Volcán Puracé, 7 = Mina de Azufre; 8 = Ricaurte, 9 = Puerres. *Ecuador:* 10 = Rio Pichan; **C:** 11 = Verdecocha, 12 = Volcán Pichincha, 13 = south side of Cayambe, 14 = Oyacachi. The open dot in the Eastern Cordillera of Colombia is Bogotá. Individuals from localities 8–10 were not included in the analysis of geographic size variation (see text). Localities were plotted with the aid of ornithological gazetteers (Paynter and Traylor, 1977, 1981).

Eriocnemis mosquera is known to occur from La Leonera, at the head of the Central Cordillera in Colombia (5°05′N) south to San Rafael on the slopes of Volcán Tungurahua in Ecuador (1°22′S, Robert Ridgely, personal commun.). Most of the specimens of *E. mos-* *quera* came from three regions, all volcanic highlands (fig. 1): in Colombia, between La Leonera and Nevado de Santa Isabel (fig. 1, loc. 1, 2), around Popayán and Volcán Puracé (loc. 3–7), and in Ecuador, from Volcán Pichincha and Volcán Cayambe (loc. 10–14).

TABLE 1
Pearson Product-moment Correlation Coefficients for the Five Mensural Characters of Adult *Eriocnemis mosquera*
EC = exposed culmen; CF = culmen from flange of nasal operculum; P = outer primary; WB = chord of wing from butt; OT = outer tail feather. Sexes are pooled.

	OT	EC	CF	P
EC	0.018	—		
CF	0.050	0.964^a	—	
P	0.675^a	−0.054	0.033	—
WB	0.480^b	−0.210	−0.130	0.864^a

$^a P < 0.001$, $^b P < 0.01$.

Two additional specimens are from the southern end of the Central Cordillera in Colombia (loc. 8, 9). There are apparently no collections from the Eastern Cordillera of Colombia, where Bogotá is located (Meyer de Schauensee, 1948).

I used only adult specimens to examine patterns of geographic variation; I did not include localities represented only by immatures (loc. 9, 10) or by a specimen that could not be aged because its bill was damaged (loc. 8). Because of small sample sizes, I pooled specimens into three geographic samples (A–C; see fig. 1) for statistical analyses. I estimated missing values for a female specimen from pooled sample B with a two-step regression using BMDP program PAM. The remaining statistical analyses were carried out with SPSS^x.

RESULTS

GEOGRAPHIC VARIATION: Several of the characters measured for this study are highly correlated (table 1) and exhibit similar patterns of geographic variation (table 2). However, the patterns of variation in bill, wing, and tail measurements are different from each other (table 2).

Bill length in both sexes exhibits a positive correlation with latitude (for males, EC: $r^2 = 0.66$, CF: $r^2 = 0.64$; for females, EC: $r^2 = 0.59$, CF: $r^2 = 0.55$; all probabilities are highly significant: $P < 0.001$). Geographic variation is clinal in males but there is no consistent directional pattern in females (fig. 2). These results are provisional, however, be-
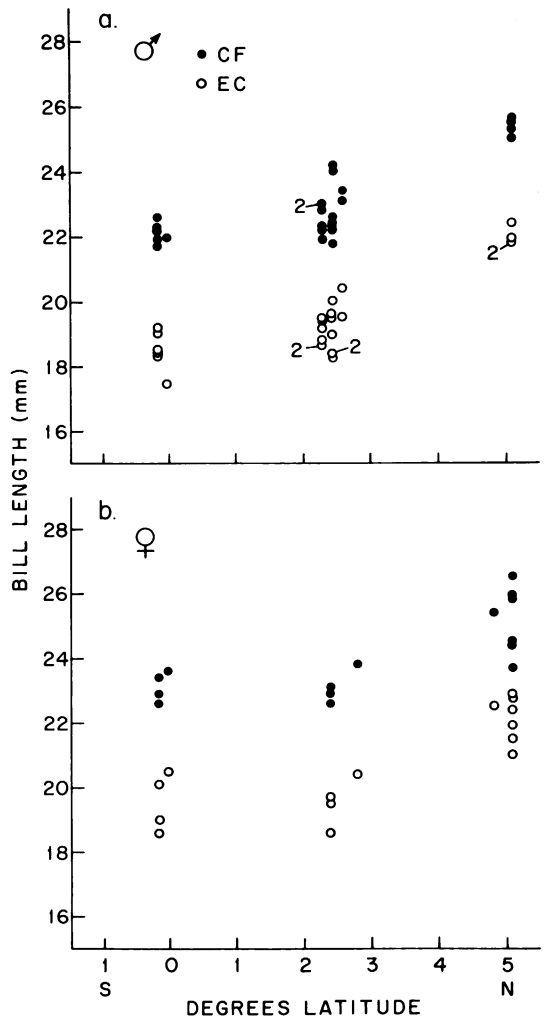

Fig. 2. Geographic variation in bill length (EC = exposed culmen; CF = culmen from flange of nasal operculum) of male (a) and female (b) *Eriocnemis mosquera*.

cause the available specimens occurred in only three widely separated geographic regions, and some sample sizes are small (e.g., N < 5). In both sexes, however, mean bill lengths are significantly longest in the northernmost sample (A), whereas mean bill lengths of the two southern samples (B, C) are similar to one another (table 2). There is, in fact, no overlap for either sex in the length of exposed culmen (EC) between the northernmost and southern samples: range for sample A is 20.9–22.9 mm; for sample B 17.5–20.5 mm. Thus, differences in bill length between the north-

TABLE 2

Means (± One S.E.) for Five Mensural Characters in the Three Pooled Geographic Samples (A–C)
Character abbreviations are as in table 1. Sexes are analyzed separately.

	Male			Female		
	A (N = 4)	B (N = 15)	C (N = 6)	A (N = 7)	B (N = 4)	C (N = 4)
EC	22.0 ± 0.14	19.1 ± 0.16	18.5 ± 0.24	22.0 ± 0.32	19.6 ± 0.37	19.6 ± 0.45
CF	25.4 ± 0.13	22.7 ± 0.18	22.1 ± 0.13	25.2 ± 0.38	23.1 ± 0.26	23.1 ± 0.23
P	53.0 ± 0.47	51.7 ± 0.32	52.6 ± 0.53	51.2 ± 0.47	50.0 ± 0.37	51.4 ± 0.54
WB	70.2 ± 0.69	69.1 ± 0.37	71.3 ± 0.58	68.2 ± 0.72	66.0 ± 1.15	69.6 ± 0.52
OT	59.1 ± 1.45	56.9 ± 1.16	55.9 ± 0.91	54.6 ± 0.60	53.7 ± 0.50	53.1 ± 1.72

Means not significantly different from each other by Scheffé a posteriori contrasts at $P < 0.05$ level are connected by underlining.

ernmost and southern samples are not an artifact of sampling or sexing of specimens.

Patterns of geographic variation in wing and tail measurements are not as pronounced as those of bill measurements. In both sexes, mean wing lengths (P and WB) are smallest in the geographically intermediate sample (B), but only male WB is significantly smaller (B from C; see table 2). In both sexes, the mean length of outer tail feather is longest in the northernmost sample (A) and exhibits a weak clinal trend that is not statistically significant (for males, $r^2 = 0.09$, $P > 0.09$; for females, $r^2 = 0.11$, $P > 0.1$) (table 2).

TAXONOMY: The difference in mean bill length between the northernmost (A) and southern (B, C) samples is consistent with the 2 to 3 mm difference mentioned by Hartert in his original description of *E. m. bogotensis* (table 2). I agree with Todd (1942) that birds from the central section of the Central Cordillera (the large series of Carriker specimens from La Leonera and Santa Isabel that comprise sample A) are greener than the more coppery colored birds from Popayán (included in sample B) and farther south.

The longer-billed birds from the central section of the Central Cordillera (northernmost sample) are thus readily distinguishable and it may be desirable to retain the name *bogotensis* for them. However, the evidence for clinal variation in bill length of males makes formal recognition of *bogotensis* unwarranted until the pattern of geographic variation can be examined with more complete sampling (see Wilson and Brown, 1953,

for a discussion of the problem of recognizing subspecies that are part of clinal patterns). In particular, collections are needed from the large gap between Santa Isabel (loc. 2, the southernmost locality of longer-billed individuals) and El Crucero (loc. 4, the northernmost locality of shorter-billed individuals in the Central Cordillera) to determine if *E. mosquera* occurs there and if so, whether the populations intergrade in a clinal pattern.

DISTRIBUTION: The information presented in this paper suggests that the range of *E. mosquera* does not include the Eastern Cordillera of Colombia; its purported occurrence there is based on the Bogotá trade skins (Chapman, 1917; Peters, 1945; Meyer de Schauensee, 1948, 1966; Hilty and Brown, 1986). It is likely that the Bogotá trade skins of longer-billed *E. mosquera* were in fact collected in the central section of the Central Cordillera. Native collectors of Bogotá trade skins sometimes worked in regions that were located at considerable distances from Bogotá, including the Central Cordillera. There are Bogotá trade skins of other taxa that occur only in the Central Cordillera (Chapman, 1917; Berlioz and Jouanin, 1944). For example, *Eriocnemis derbyi longirostris*, like Hartert's *E. m. bogotensis*, was described from Bogotá trade skins. In Colombia, however, *E. derbyi*, including *E. d. longirostris*, is known only from the Central Cordillera (Hilty and Brown, 1986). Chapman (1917) concluded that the Bogotá trade skin specimens of *E. d. longirostris* probably came from the Quindío trail region of the Central Cordillera, which

is located at about the same latitude as Bogotá (4°36′N), across the Magdalena River valley (fig. 1). It is therefore very likely that the central section of the Central Cordillera, where long-billed *E. mosquera* occurs, was visited by the native collectors who brought their skins back to Bogotá. Significantly, Olivares (1969) did not list *E. mosquera* in his comprehensive work on the birds of Cundinamarca, the department where Bogotá is located.

DISCUSSION

Eriocnemis mosquera is one of many Andean hummingbirds adapted to high-altitude shrubby and forested habitats (generally occurring above 2500 m). Patterns of variation in this species underscore several patterns in the distribution and differentiation of high-elevation birds in the northern Andes.

The evidence that *E. mosquera* does not occur in the Eastern Cordillera, as presented here, is consistent with the distributions of other highland birds of the Central Cordillera. Many of these species occur from the Central Cordillera farther south, but they rarely occur in the Eastern Cordillera (Meyer de Schauensee, 1966). This pattern is probably due to the presence of deep river valleys between the Cordilleras, and to the absence of high-altitude habitats (over 3000 m) in the Eastern Cordillera where it joins the Central Cordillera (Vuilleumier, 1971). These barriers effectively isolate the high-altitude avifauna of the Central Cordillera, and should promote differentiation among representative forms in the different ranges. Indeed, many high-altitude species from the Central Cordillera are replaced by related species in the Eastern Cordillera (Chapman, 1917). Thus, *Eriocnemis mosquera* appears to be closely related to *E. cupreoventris,* a species with similar plumage in the Eastern Cordillera.

Eriocnemis mosquera also adds to the number of highland birds that are differentiated within the Central Cordillera; see Vuilleumier and Simberloff (1980) for a list of cases. Hummingbird examples include (differentiated taxon in brackets): *Heliangelus exortis exortis* (Bleiweiss, 1985), *Coeligena lutetiae* (Bleiweiss, in prep.), *Eriocnemis der-*byi (*longirostris*), *Metallura williami* (*williami*) (Chapman, 1917; Vuilleumier and Simberloff, 1980; Hilty and Brown, 1986), *Chalcostigma herrani* (*tolimae*) (Kleinschmidt, 1927; Vuilleumier and Simberloff, 1980), and *Acestrura heliodor* (Graves, 1986). Differentiation in these additional species is similar to that in *E. mosquera*: it is intraspecific, and in some cases clinal (e.g., a positive correlation of wing and tail length with latitude in *Acestrura heliodor*; see Graves, 1986). Moreover, many of these endemic forms of the Central Cordillera occur on the páramo island of the Nevados del Tolima and Ruiz (Tolima-Ruiz) (Vuilleumier, 1970, 1979; Vuilleumier and Simberloff, 1980; Simpson Vuilleumier, 1971).

These concordant patterns suggest that extrinsic factors have produced differentiation among populations within the Central Cordillera. One explanation for the occurrence of so many differentiated forms on the Tolima-Ruiz páramo is that this region provided a refuge of suitable habitat in which populations of highland-adapted birds differentiated in isolation during Pleistocene glacial cycles. The relatively minor differentiation may be due to the incomplete isolation of this region; even during the present interglacial time, which should favor isolation of highland-adapted forms, the Tolima-Ruiz páramo is connected to more southern páramos by a narrow bridge of highland vegetation (Vuilleumier and Simberloff, 1980). Presumably, complete isolation of this páramo can occur only during extreme interglacial conditions. The region may also promote differentiation without physical isolation by virtue of an unusual ecological regime: clinal patterns such as in *E. mosquera* and *A. heliodor* can evolve even under extensive gene flow along a strong environmental gradient (Endler, 1977).

A factor that may promote differentiation through the creation of either physical barriers to gene flow or strong selection gradients is active volcanism. This is a well-documented phenomenon in the Central Cordillera, including the area around Nevado del Ruiz (Folster et al., 1977). Several authors have suggested that the dark plumage of birds that inhabit areas of recent volcanic activity is an adaptation to match the darkened vege-

tation (Johnson and Brush, 1972; Graves, 1982). Structural and taxonomic characteristics of the vegetation are known to affect hummingbird foraging behaviors (Feinsinger and Colwell, 1978; Hixon et al., 1983), so the alteration of habitat by volcanic eruptions might also induce changes in hummingbirds' trophic structures (bills, as in *E. mosquera*).

Patterns of differentiation among populations within the Cordilleras of Colombia are not as well documented as are those between populations in different Cordilleras. It is noteworthy that differentiation among highland bird populations within the Central Cordillera is predominantly infraspecific and often clinal since divergence between representative forms in the different Cordilleras is usually discontinuous and suggests incipient or completed speciation (Chapman, 1917; Vuilleumier and Simberloff, 1980). Examination of the consistency of these differences should be an aim of future studies of speciation in the northern Andes.

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APPENDIX

Adult specimens of *Eriocnemis mosquera* used in the analysis of geographic variation. The acronyms for museums are defined in the Acknowledgments.

Colombia: La Leonera: ANSP 73746, CM 70491, 70504, 70536–37, 70540, 70626–27, 70632, 70742; Santa Isabel: AMNH 111613; Coast Range West of Popayán: AMNH 109474; El Crucero (Cauca): FMNH 226528–29, 226531, LACM 31293, 31296–97, 362219–20, WFVZ 13177–78; Páramo San Rafael: LACM 33345–46; Volcán Puracé: ANSP 142606, LSUMZ 38576–77, 44669, USNM 446235, WFVZ 13175–76; Mina de Azufre: CM 137432.

Ecuador: Verdecocha: MLOC 1796; Volcán Pichincha: ANSP 65394, USNM 174457, 174459–62, 174465; Cayambe: MLOC 1797; Oyacachi: AMNH 180073.