ZOOGEOGRAPHY AND GEOGRAPHIC VARIATION OF *PLATYRINCHUS MYSTACEUS* IN BOLIVIA AND PERU, AND THE CIRCUM-AMAZONIAN DISTRIBUTION PATTERN

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Abstract. In South America, *Platyrinchus mystaceus* (Tyrannidae) is found in the Tepui region, the Coastal Range of Venezuela, the humid Andes, and the lowlands of southcentral and southeastern South America. Recent discoveries of new localities in the lowlands of Bolivia and in the southern Andes of Peru fill two huge gaps in the previously known distribution, which encircles the Amazonian-Guianan forest region. This pattern, here called the Circum-Amazonian pattern, is found in a number of other species and species groups of birds. An analysis of plumage shows that the newly discovered populations in the southern Andes are intermediate in ventral coloration between populations to the north and south. Populations of *P. mystaceus* in the Andes south of the equator are increasingly ochraceous with increasing distance from the equator, a pattern found in many species of Andean birds. Geographic variation in size shows a bimodal pattern and does not conform to Bergmann's "Rule". In the lowlands, specimens from the newly discovered site nearest to the Andes show phenotypic evidence of gene flow from the nearest Andean population. *Accepted 22 August 1991.*

Key words: Platyrinchus mystaceus, Tyrannidae zoogeography, South America, Andes, geographic variation.

THE CIRCUM-AMAZONIAN DISTRIBUTION PATTERN

The distribution of *Platyrinchus mystaceus* (White-throated Spadebill; Tyrannidae) in South America shows a "circum-Amazonian" pattern. This species is found (Fig. 1; summarized from Traylor 1979) at lower elevations in the Andes from Venezuela and Colombia (where not recorded from most of the Eastern Andes) south to central Bolivia, with isolated populations in other montane regions north of the Amazon Basin, namely the Tepuis and the Coastal Range of northern Venezuela. It is also found in lowland areas peripheral to the Amazon Basin in eastern Brazil from Maranhão, Ceará, Alagoas, and Paraíba south along the coastal region of southeastern Brazil to Santa Catarina, then extending west into northeastern Argentina (Misiones and Corrientes), eastern Paraguay, and Brazil south of the Amazon basin in Goiâs and Mato Grosso.

We define the circum-Amazonian distribution pattern as one in which sister taxa are found in (a) *montane* forested areas on the humid slopes of the Andes and the Coastal Range of Venezuela or the Tepui region, and (b) *lowland* forested areas south and east of the lowland forests of Amazonia. We distinguish this pattern from that shown by a few lower montane species that are restricted to humid mountains around the periphery of Amazonia that are not found in the *lowlands* in the southeastern portion of the range (e.g., *Laniisoma elegans* [Cotingidae]).

The circum-Amazonian pattern is found in several other bird species and species-groups, including other tyrannids. Fitzpatrick & O'Neill (1979) illustrated such a pattern for a group of sister species within the genus *Hemitriccus*. Using the distributions of tyrannids given by Traylor (1979), we found two other species with this pattern: *Phyllomyias (Acrochordopus) burmeisteri* and *Hirundinea ferruginea*. We also found another six species and species-groups that showed a portion of the pattern, with populations present in the Andes and in the lowlands south and east of Amazonia but absent from the northern Andes, northern Venezuela, or the Tepuis:

FIG. 1. Distribution of *Platyrinchus mystaceus* in South America.

Elaenia albiceps - E. parvirostris, E. obscura, Myiornis auricularis - M. albiventris, Todirostrum plumbeiceps, Knipolegus signatus - K. cyanirostris, and *Pachyramphus validus.* Also, the members of the genus *Phylloscartes* (*sensu strictu*) together show the complete pattern. Using the distributions for the Formicariidae and Rhinocryptidae given by Peters (1951), we found four examples of the complete pattern (*Dysithamnus mentalis,* the sister taxa *Myrmotherula behni - M. grisea - M. unicolor* [see also Hackett & Rosenberg 1990], *Chamaeza campanisona,* and the members of the genus *Scytalopus*) and six examples of a partial pattern (*Batara cinerea, Thamnophilus caerulescens, T. ruficapillus,* the *Herpsilochmus pileatus - H. atricapillus* species group (see also Davis & O'Neill 1986), *H. rufimarginatus,* and *Pyriglena leuconota*). Using the maps in Isler & Isler (1987) for the Thraupinae, we found four examples of a nearly complete circum-Amazonian pattern: *Piranga flava, Pipraeidea melanonota, Euphonia musica,* and *Chlorophonia cyanea.* Therefore, we conclude that although the pattern is uncommon, it is widespread among passerines.

For taxa that show the circum-Amazonian pattern, Bolivia is of zoogeographic interest because it is there where a montane representative meets or comes closest to meeting a lowland representative. As we will document in the following sections, our recent fieldwork has clarified the Bolivian distribution of *Platyrinchus mystaceus* by filling the gap between montane and lowland populations (Fig. 2).

ZOOGEOGRAPHY AND GEOGRAPHIC VARIATION IN PLUMAGE IN THE ANDES OF PERU AND BOLIVIA

The most recent summary of the distribution of the subspecies of *Platyrinchus mystaceus* (Traylor 1979) listed only one subspecies in Bolivia, *P. m. partridgei,* this known from just six specimens in two departments, Cochabamba and Santa Cruz (Short 1969). Remsen, the Schmitts, and other personnel from the Museum of Natural Science, Louisiana State University (LSUMZ), collected *P. m. partridgei* at three localities in Dpto. La Paz, all in lower montane forest on the Serranía Bellavista in Prov. Nor Yungas: (1) 47 km by road north of Caranavi, 1350 m elevation, 12—27 July 1980 (N = 8); (2) 37 km by road north of

Caranavi, 1625 m, 28 June 1979 (N = 1); and (3) 35 km by road north of Caranavi, 1650 m, 16 June—2 July 1989 (N = 3). All these specimens, with their distinctive bright ochraceous underparts, match Short's (1969) description of *partridgei.* We also note that placement of one of the three previously known localities of this subspecies in Dpto. Cochabamba is apparently an error. "San Juan Mayo" is presumably the same as "San Juan Mayu", which was located in Dpto. La Paz by Paynter et al. (1975) at 2000 m, northeast of Irupana in Prov. Sud Yungas.

The Schmitts also collected *P. m. partridgei* in southwestern Dpto. Santa Cruz in humid forest at 13 km by road northwest of Masicuri, 1000 m, Prov. Valle Grande, on 13 July 1984. This is approximately 130 km south of the only previously known locality (Cerro Hosane) in Dpto. Santa Cruz.

Additionally, we report here the first specimens of *P. m. partridgei* from Peru. An LSUMZ team (T.S. Schulenberg, L.C. Binford, and others) collected two specimens on 12 and 29 November 1980 in Dpto. Puno in humid montane forest at Abra de Maruncunca, 2000 m, 10 km southwest of San Juan del Oro, just a few kilometers from the Bolivia border. These specimens are indistinguishable from our series from Serranía Bellavista. Therefore, recent LSUMZ field-

FIG. 2. Distribution of *Platyrinchus mystaceus* Bolivia.

work has extended the range of this taxon approximately 225 km north.

We also report the first specimens of *P. mystaceus* from the southern Andes of Peru in dptos. Cuzco and Madre de Dios. Together with the specimens reported above, the new localities in the Andes fill a gap in the species' previously known Andean distribution nearly 650 km in length. Many specimens from Cuzco and Madre de Dios are intermediate between *P. m. zamorae* of northern and central Peru and *P. m. partridgei* in their ventral coloration. The bellies of many of these specimens are notably tinged with a more ochraceous yellow, and the breast and flanks are a brighter, less olivaceous brown than are those of more northerly *zamorae*, but they are not as ochraceous as *partridgei*. Two specimens from Dpto. Pasco, within the previously known range of *zamorae*, also tend towards *partridgei* in ventral coloration. However, two specimens from Tono, Dpto. Cuzco, are indistinguishable from those of *zamorae* from Dpto. Huánuco north to Dpto. Amazonas, and one specimen from Dpto. Amazonas and two from Dpto. San Martín are not distinguishable from the more richly colored specimens from Pasco, Cuzco, and Madre de Dios.

Thus, our interpretation of the specimen data currently available is that there is a cline in coloration in the populations of the Peruvian Andes. From south of the Marañon River from Dpto. Amazonas 600 km south to Dpto. Huánuco, most specimens are brownish-breasted and yellowish-bellied, but some specimens (3 of 26 specimens examined) show more ochraceous ventral coloration. From Dpto. Pasco 525 km south to Dpto. Cuzco and western Dpto. Madre de Dios, most specimens show characters intermediate between typical *P. m. zamorae* and *P. m. partridgei*, but some specimens are identical to those from farther north (2 of 19 in our sample). Seven of the 19 specimens from this region have slightly more reddish backs than either *zamorae* from farther north or *partridgei*. From southern Dpto. Puno, Peru, to southwestern Dpto. Santa Cruz, Bolivia, is found an ochraceous-bellied population, *P. m. partridgei*, that does not show any obvious change in color over this 750-km-long range. All 13 specimens in our sample from this range can be distinguished with 100 % certainty from those from farther north by the combination of bright ochraceous underparts and slightly greener backs. The phenotypic intermediacy of the population from Pasco to Cuzco presumably represents gene flow between *zamorae* and *partridgei*.

Another interpretation of the pattern of phenotypic variation is that the clinal variation in plumage is caused by natural selection. *Platyrinchus mystaceus* is one of many species and superspecies of Andean birds of the humid eastern slope whose southermost populations show increasing amounts of ochraceous, buffy, rufous, or rusty coloration relative to duller, more olivaceous, darker reddish, or darker brown populations closer to the equator (Remsen, unpubl. data). For example, of the 11 species and superspecies in the Furnariidae that exhibit geographic variation in coloration and that are found on the humid slopes of the Eastern Andes as far south as Bolivia, 9 show this pattern of geographic variation: *Synallaxis azarae - S. superciliosa* (Remsen et al. 1988), *Cranioleuca albiceps* (Remsen 1984a), *Schizoeaca* spp. (Remsen 1981), *Cranioleuca curtata*, *Asthenes urubambensis*, *Margarornis squamiger*, *Premnoplex brunnescens*, *Anabacerthia striaticollis*, and *Thripadectes flammulatus - T. scrutator* (data from Cory & Hellmayr 1925, Fjeldså & Krabbe 1990, Remsen unpubl.). Although there is evidence that many other patterns of color variation in Andean birds do not have an adaptive basis (Remsen 1984b), such parallel variation in independent lineages implies an underlying adaptive reason for the pattern. One hypothesis for the adaptive basis of this pattern is that it is related to background matching: if the dry season is longer or more severe in the southern humid Andes, then perhaps the forest there has a more "rusty", less greenish overall aspect than Andean forest at more equatorial latitudes. Unfortunately, weather data from the eastern slope of the Andes are virtually nonexistent, and we have no measurements of overall color aspect of forests at different latitudes.

In *P. mystaceus*, the range of the population with intermediate coloration is nearly as long as that of *P. m. partridgei* and far larger than that typically associated with zones of intergradation. Therefore, the possibility that this population

deserves recognition as a discrete entity, a subspecies, needs to be addressed. Remsen tested the distinctiveness of this population by asking four ornithologists to match all specimens to a typical example of each of the three populations: (1) *zamorae* from Amazonas to Huánuco, (2) the possible new subspecies from Pasco to Cuzco, and (3) *partridgei* from Puno to Santa Cruz. Although all observers were able to identify all properly prepared specimens of *partridgei* correctly, all four placed 2 (13%) of the 16 specimens from the possible new taxon with the specimens of *zamorae* from Huánuco to Amazonas. These two specimens were the same in all four trials: both specimens from Tono, Dpto. Cuzco. The average number of specimens of the sample of 25 *zamorae* from Amazonas to Huánuco that were placed with the Pasco-to-Cuzco population was 4.5 (range 3 to 7), or 18% of the specimens. The combined average percent of specimens that were not "properly" classified was 16%. Therefore, the Pasco-to Cuzco population is not a discrete entity that merits a formal name. Whether this population should be assigned to *P. m. zamorae*, noting that this taxon shows clinal variation in Peru south of the Marañon River, or whether the Pasco-to-Cuzco population should be designated as a zone of intergradation 525-km-long between *zamorae* and *partridgei* would seem to be an arbitrary decision.

The specimens from the newly discovered portion of the range of *zamorae* are as follows (all collected by J. W. Fitzpatrick, D. E. Willard, and other personnel of the Field Museum of Natural History; see Stephens & Traylor [1983] for details of localities not in quotes): *Dpto. Cuzco*: Tono, 870 m (N = 2); Consuelo, 1200 m (2), 1330 m (1), 1380 m (2). *Dpto. Madre de Dios*: Cerro de Pantiacolla, above Río Palotoa, 1075 m (1), 1350 m (1); Cerro de Pantiacolla, E. slope near summit, about 4 km east of Shintuya, 980 m (1); "ridge above Hacienda Amazonia", 780 m (1), 815 m (1), 900 m (1), and 1050 m (1).

GEOGRAPHIC VARIATION IN SIZE IN THE ANDES OF PERU AND BOLIVIA

We recorded body mass (from specimen labels) and measured wing lengths (wing chord to nearest 0.1 mm with dial calipers) as indices of body size for all specimens in our sample. Use of body
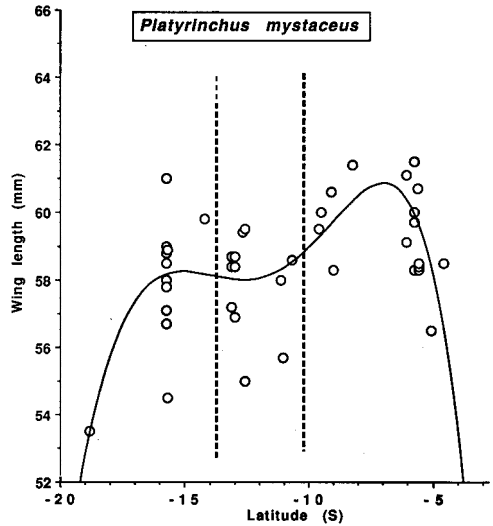

FIG. 3. Geographic variation in wing length of male *Platyrinchus mystaceus* in the Andes from northern Peru to central Bolivia. The line represents a fifth-order polynomial fitted to the points (r^2 = 0.412, P = 0.001). The vertical dashed lines represent the boundaries between three populations (see text).

mass as an index of size has many problems, especially for small birds such as *P. mystaceus* that are not measured precisely by the types of scales used in fieldwork. Furthermore, the weights themselves were taken by numerous different preparators using a variety of types of scales that were not intercalibrated, and for a species such as *P. mystaceus* that weighs approximately 10 grams, those individuals below 10 g are usually weighed with a 10-g scale, whereas those above 10 g are weighed on 30- or 50-g scales. In nonmigratory species found in habitats of similar degrees of openness throughout their range, wing length presumably provides a good estimate of body size. Although body mass and wing length did not correlate significantly in our sample (males, r^2 = 0.053, P = 0.184; females, r^2 = 0.305, P = 0.098), both measures showed the same patterns of geographic distribution as outlined below. Our sample size of females was so small and so geographically limited (e.g., only one from Bolivia) that only males were used in the analyses below.

From northern Peru to central Bolivia, *P. mystaceus* shows a slightly bimodal pattern of geographic variation in wing length and body mass. The two peaks correspond to the latitudes occupied by *partridgei* in Dpto. La Paz and by *zamorae* in dptos. San Martín and Amazonas (Fig. 3). Such local peaks and valleys are found regularly in patterns of geographic variation in size in Andean birds, the vast majority of which do not show size variation corresponding to the pattern predicted by Bergmann's "Rule" (Remsen & Wiedenfeld, unpubl. data). The variation in size among the three populations is statistically significant (Kruskal-Wallis, H = 7.83, P < 0.02). Wing length and body mass show weak but significantly negative decreases (wing length, r^2 = --0.197, P = 0.0028; body mass, r^2 = −0.129, P = 0.034) with increasing latitude away from the equator, the opposite from the prediction of Bergmann's Rule. There were no statistically significant correlations between wing length and elevation (r^2 = 0.025, P = 0.32) or between latitude and elevation (r^2 = 0.066, P = 0.10).

ZOOGEOGRAPHY AND GEOGRAPHIC VARIATION IN PLUMAGE IN THE BOLIVIAN LOWLANDS

The first specimen of *Platyrinchus mystaceus* from the lowlands of Bolivia was collected by the Schmitts in forest 6 km by road southeast of Trinidad, 175 m, Dpto. Beni, on 30 October 1984 (LSUMZ 124442). With its bright yellow underparts, greenish upperparts, and pale mandible, this specimen matches closely two specimens of *P. m. bifasciatus* from the type locality, Chapada, Mato Grosso, Brazil, almost 950 km east-southeast of Trinidad. The only differences are that the yellow of the Mato Grosso specimens is slightly duller and the maxilla is not as black, differences possibly attributable to the 100-year difference in the specimens' ages. We tentatively assign the Trinidad specimen to *bifasciatus*.

A second lowland locality was discovered by Rocha in Dpto. Beni at the Estación Biológica Beni, 200 m, Prov. Yacuma, where three specimens were collected in second-growth forest at two sites on 24 and 31 July, and 11 October 1988. In contrast to the Trinidad specimen, these three specimens are more ochraceous below, and in

this respect they appear to approach *partridgei*. In other respects (color of upperparts and mandible, wing length of male), they are like lowland *bifasciatus*. This locality is only 150 km from the foothills of the Andes at Serranía Bellavista, where *partridgei* is found.

A third locality in the lowlands was recently discovered by Parker & Rocha (1991) in extreme eastern Dpto. Beni near the border with Brazil at the base of the Cerro San Simón, Prov. Itenez. Although tape-recordings documented the identification at the species level (deposited at Library of Natural Sounds, Laboratory of Ornithology, Cornell University), subspecies could not be determined because no specimens were obtained. All three lowland localities in Bolivia are at the periphery of the species-rich Amazonian forest to the north. Together they dramatically reduce the previous, nearly 1200-km-long gap between lowland and Andean populations of *P. mystaceus*.

As with specimens from the Andes of central-southern Peru, the phenotypic intermediacy in underparts coloration of the Beni Station birds may be interpreted as representing gene flow between highland and lowland populations. This is consistent with the current taxonomic treatment of these forms as subspecies of a polytypic species. Also consistent with this interpretation is that the vocalizations of all populations of *partridgei*, other Andean forms farther north of *partridgei*, the lowland forms in southeastern Brazil, and whichever form is at the Cerro San Simón are all similar to the ear (T. A. Parker, pers. comm.). Vocal differences between phenotypically similar tyrannids are often indicators of reproductive isolation and are regarded as species-level differences (e.g., Lanyon 1967, 1978; Johnson 1963; Johnson & Marten 1988).

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