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SPECIES LIMITS IN MESOAMERICAN *AULACORHYNCHUS* TOUCANETS

ADOLFO G. NAVARRO S.,^{1,3} A. TOWNSEND PETERSON,²
ESTEBAN LÓPEZ-MEDRANO,¹ AND HESQUIO BENÍTEZ-DÍAZ¹

ABSTRACT.—We examined geographic patterns of variation and differentiation in morphological characters of the emerald toucanets (*Aulacorhynchus* spp.) of Mesoamerica. Bill lengths showed flat frequency distributions, suggesting that no “adult” size is reached, and raising the possibility that bill growth in toucanets may be indeterminate. Sparse lowland populations in the Petén region are of uniformly small body size, suggesting that they may consist of subadult individuals. Patterns of variation support recognition of four species in Mesoamerica: *A. wagleri* in western Mexico, *A. prasinus* in eastern Mexico and northern Central America, *A. caeruleogularis* in Costa Rica and western Panama, and *A. cognatus* in eastern Panama, as well as several additional forms (*A. lautus*, *A. albivitta*, and *A. nigrogularis*) in South America.

RESUMEN.—Se analizaron los patrones de variación y diferenciación de los caracteres morfológicos en las tucanetas (*Aulacorhynchus*) de Mesoamérica. La longitud del pico mostró una distribución de frecuencias plana, lo que sugiere la posibilidad de que nunca se alcanza un tamaño “adulto” y, por lo tanto, el crecimiento del pico en las tucanetas es indeterminado. Las escasas poblaciones de las tierras bajas en la región del Petén son uniformemente pequeñas en tamaño corporal, sugiriendo la posibilidad de que estén constituidas por individuos subadultos. Los patrones de variación apoyan el reconocimiento de cuatro especies en Mesoamérica: *A. wagleri*, del oeste de México, *A. prasinus* del este de México y norte de Centroamérica, *A. caeruleogularis* de Costa Rica y el oeste de Panamá, y *A. cognatus* del este de Panamá, con varias formas adicionales (*A. lautus*, *A. “albivitta”* y *A. “nigrogularis”*) en Sudamérica. *Received 30 Nov. 2000, accepted 12 Dec. 2001.*

The toucans (family Ramphastidae, subfamily Ramphastinae) are a diverse group of 35 species of Neotropical frugivores that often

exhibit strikingly abrupt patterns of geographic variation or restricted geographic distributions. The toucanets of the genus *Aulacorhynchus*, currently placed in six or seven polytypic species (Peters 1948, Sibley and Monroe 1990), are among the most interesting of the toucans. They are almost completely restricted to humid montane forests, they show wild patterns of discrete variation in coloration and size, and several isolated populations on sin-

¹ Museo de Zoología, Facultad de Ciencias, Univ. Nacional Autónoma de México, Apartado Postal 70–399, México DF 04510, México.

² Natural History Museum, Univ. of Kansas, Lawrence, KS 66045, USA.

³ Corresponding author;
E-mail: fcvg01@servidor.unam.mx

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FRONTISPIECE. Three forms of the Emerald Toucanet (*Aulacorhynchus prasinus*) complex. (Top) Emerald Toucanet (*A. prasinus*) from eastern Mexico to Nicaragua, (middle) Wagler’s Toucanet (*A. wagleri*) from southwestern Mexico, and (bottom) Blue-throated Toucanet (*A. caeruleogularis*) from Costa Rica and western Panama. From an original mixed painting by Marco Antonio Pineda-Maldonado.

gle mountaintops are surprisingly distinct (Haffer 1974). Systematic study of this genus, however, has been plagued perpetually by the paucity of specimens throughout its range (Peterson et al. 1998), and the lack of adequate series from any single site.

The most recent and thorough treatment of *Aulacorhynchus* was by Haffer (1974), who presented a broad overview of patterns of variation in the genus. Haffer's review was, however, mainly textual, with little quantitative analysis, and he focused on South American populations, treating Mesoamerican forms only cursorily.

The objective of the present paper is to complement Haffer's work by focusing on patterns of geographic variation in the *Aulacorhynchus* toucanets of Mexico and Central America, with the aim of clarifying the status of the western Mexican form *wagleri*. This form was described originally as a species separate from the eastern Mexican form, *prasinus*, by Sturm (1841), and was maintained as such in the detailed monographic treatments of Sclater and Shelley (1891), Ridgway (1914), and Cory (1919), the first two of whom correctly summarized the characters that distinguished it. Peters (1948), however, placed *wagleri* within the broadly distributed *A. prasinus*, and the form was thereafter forgotten as a species in avian taxonomy. Similarly, Peters placed the strikingly distinct form *caeruleogularis* in the synonymy of *A. prasinus*. In fact, Haffer (1974: Fig. 16.5) incorrectly depicts black coloration of the base of the bill of *wagleri*, hiding its most obvious distinguishing character.

METHODS

We examined and measured 247 adult-plumaged specimens of *Aulacorhynchus* toucanets from Mesoamerica, plus an additional 58 specimens from South America to place Mesoamerican patterns in a genus wide context. These specimens are housed in the American Museum of Natural History, California Academy of Sciences, Cornell Univ., Field Museum of Natural History, Inst. de Biología of the Univ. Nacional Autónoma de México (UNAM), Los Angeles County Museum of Natural History, Louisiana State Univ. Museum of Natural Science, Moore Lab. of Zoology at Occidental College, Museo de Zoología of the Facultad de Ciencias of UNAM, U.S. National Museum of Natural History, Univ. of California at Los Angeles, Univ. of Kansas Natural History Museum, and Western Foundation of Vertebrate Zoology.

From each specimen we recorded, in addition to label data, the following information: bill length, width, and depth (all measured from the plane of the anterior edge of the nostril); tarsus length (to lowest undivided scute on tarsus); wing chord; tail length (longest rectrix measured from middle base of tail); overall pattern of coloration of bill ("bill pattern"; Fig. 1); color of the rough basal portion of mandible ("color of base of mandible"); and colors of throat and superciliary region. Coloration patterns were standardized to drawings and photographs of each type.

We analysed specimen data using 10 geographic units of Mesoamerica (Fig. 2 top). South American data were organized into seven additional units (Fig. 2 bottom); these units follow the biogeographic scheme of Morrone (1999), which represents natural units geographically delimited, containing similar environmental conditions and endemic taxa.

We included all described and currently recognized subspecific forms in the study except *A. prasinus dimidiatus*; also excluded for lack of specimen material was the disjunct population of Los Tuxtlas, Veracruz, recently described as the subspecies *A. prasinus warneri* (Winker 2000).

RESULTS

The geographic distribution of specimens examined indicates an almost complete restriction of *Aulacorhynchus* toucanets to humid montane forests (Fig. 2). Each major mountain range holds a set of populations that we have grouped into geographic units for analysis, attempting to reflect continuity of populations. The only populations in the Mesoamerican lowlands are those of the Petén region in Mexico, Belize, and Guatemala.

Analyses of the largest single geographic sample available to us, that of Chiapas, indicated no sexual differences in coloration, but significant sexual differences in three of the six mensural characters (Mann-Whitney *U*-test, $n = 58$, $P < 0.05$), as previously reported for the Costa Rican populations (Skutch 1967, Riley and Smith 1992). Therefore, coloration characters were analyzed with the complete sample available, whereas mensural characters were analyzed with sexes separated. Because tests of skewness and kurtosis indicated significant departures from normality in most characters, nonparametric tests were employed throughout.

Qualitative characters showed discrete patterns of variation among populations (Fig. 3). In three of the four characters (bill pattern, color of superciliary region, and color of base of mandible), the populations of western Mex-

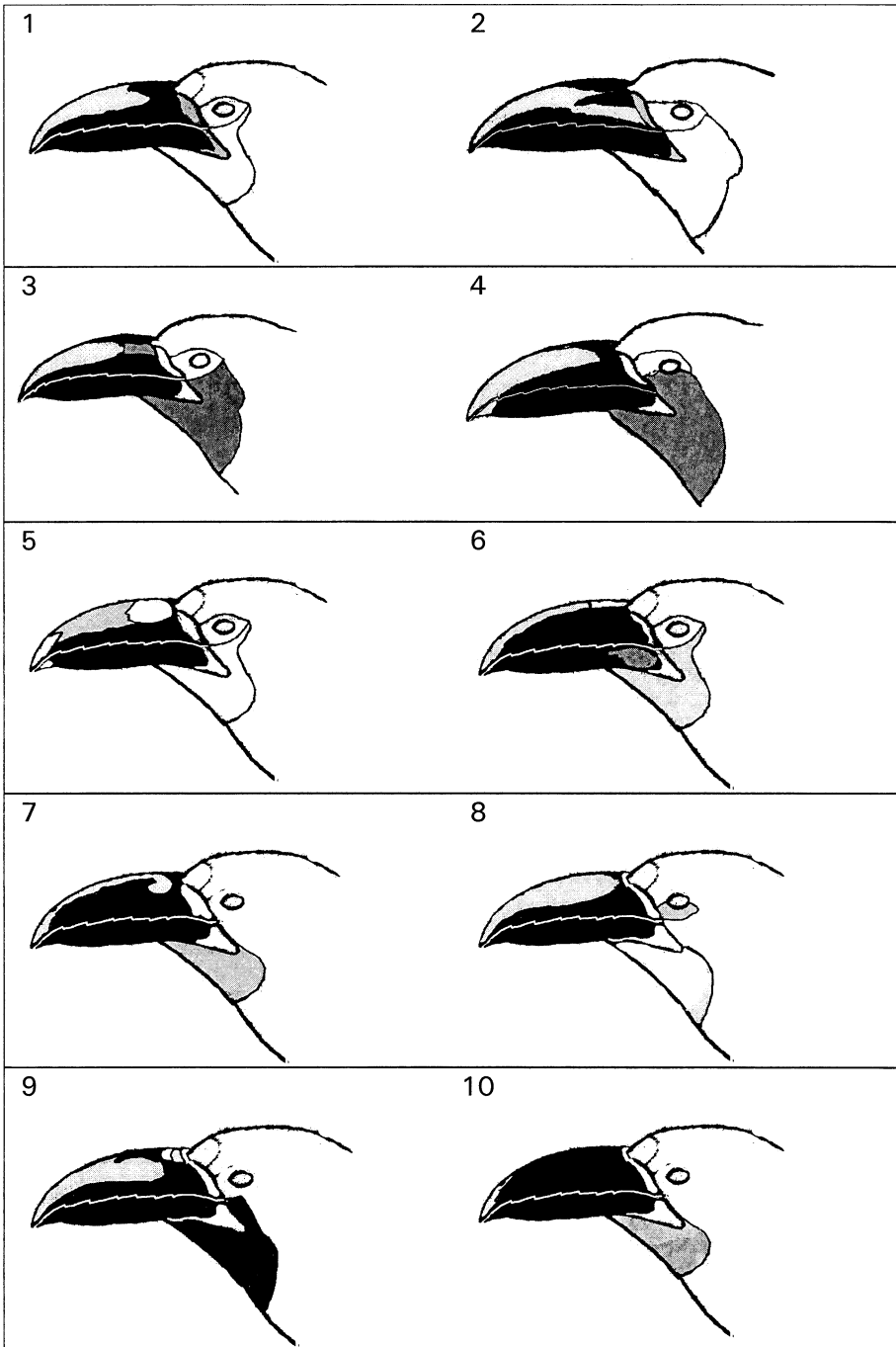


FIG. 1. Simplified representation of bill patterns of *Aulacorhynchus* toucanets. Sketches are based on the following specimens: (1) Pattern A, (LSUMZ 33135, México, Oaxaca); (2) Patterns B and C (LSUMZ 11245, México, San Luis Potosí); (3) Pattern D, blue throat (LSUMZ 68696, Costa Rica, Puntarenas); (4) Pattern E, blue throat (AMNH 135520, Panama, Mt. Tacarcuna); (5) Pattern G, white throat (LSUMZ 61505, Colombia, Santander, above Surutá); (6) Pattern I, gray throat (AMNH 108880, Colombia, Cauca, E Palmira); (7) Pattern L, light gray throat (AMNH 71352, Colombia, Santa Marta); (8) Pattern M, white throat with gray edging (AMNH 186357, Ecuador); (9) Pattern N, black throat (LSUMZ 123738, Bolivia, Beni, Serranía Pilón); and (10) Pattern P, grayish-blue throat (AMNH 18126, Peru, Chaupe).

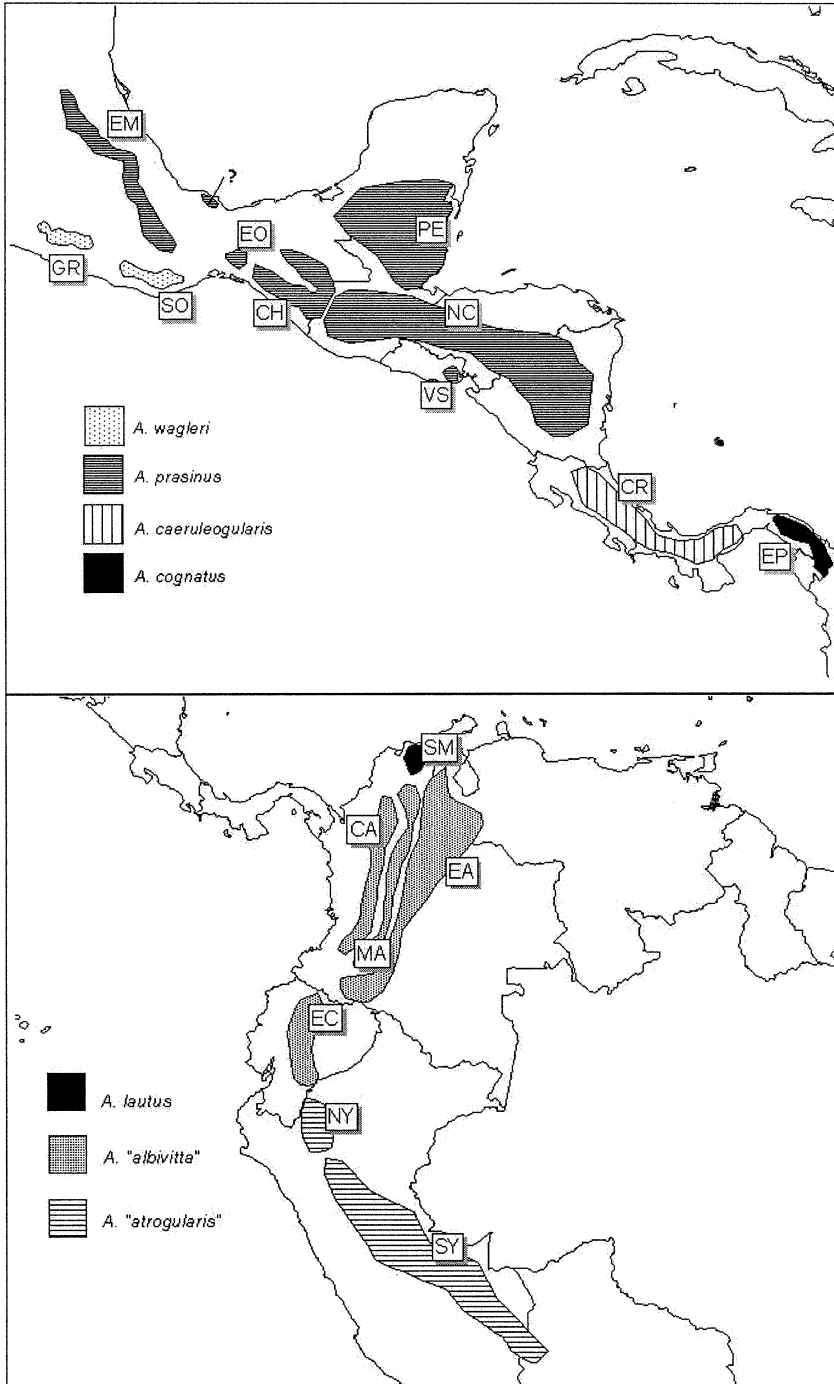


FIG. 2. Distribution of *Aulacorhynchus* toucanet populations in (top) Mesoamerica and (bottom) South America, with stippled patterns representing the ranges of herein recognized biological species. Abbreviations indicate the geographic units used for analysis: GR, Guerrero; SO, southern Oaxaca; EM, eastern Mexico; EO, eastern Oaxaca; CH, Chiapas; PE, Petét; NC, northern Central America; VS, Volcán San Miguel; CR, Costa Rica-Western Panama; EP, eastern Panama; SM, Sierra de Santa Marta; CA, Cauca Region; EA, Eastern Andes; MA, Magdalena Basin; EC, Ecuador; NY, northern Yungas; and SY, southern Yungas. Question mark indicates that no specimen from Los Tuxtlas region was available.

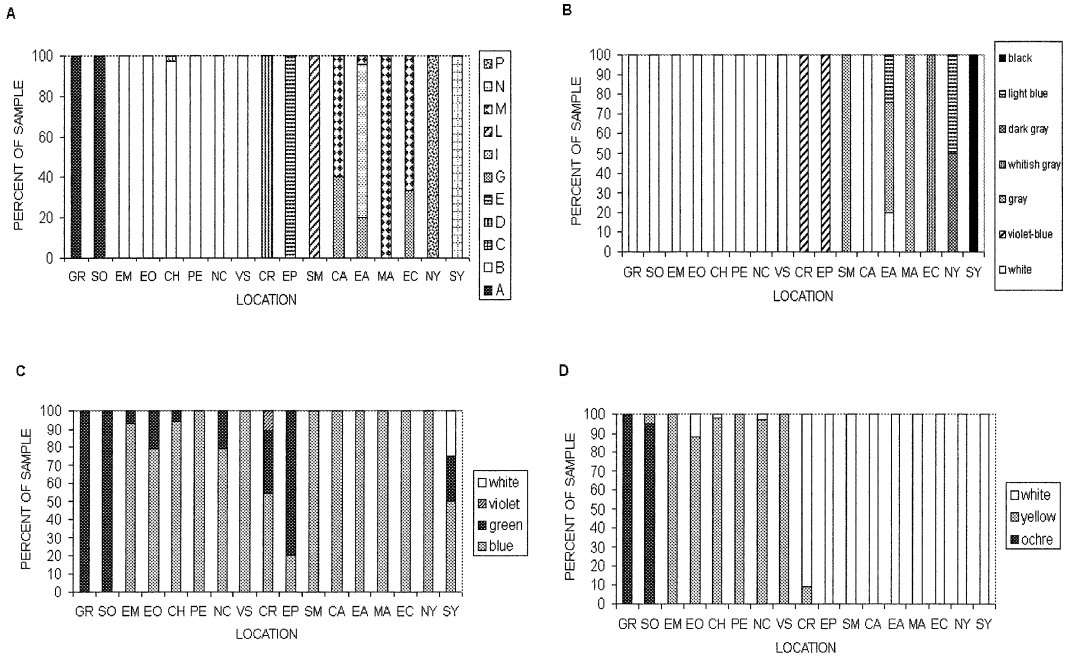


FIG. 3. Frequencies in *Aulacorhynchus* populations of four characters of coloration and external morphology, expressed as percentages of the sample examined. Each fill pattern represents a different pattern or color for a particular character. (A) Bill pattern, (B) superciliary color, (C) color of base of mandible, and (D) throat color. Bill pattern codes for Mesoamerican populations are given in Fig. 1. Population abbreviations are given in Figure 2.

ico had a state fixed or nearly fixed that was not or only rarely found in adjacent populations in eastern Mexico. One fixed character (bill pattern) distinguished the populations of Costa Rica and western Panama from those to the north, and another (bill pattern) distinguished the populations of eastern Panama. Curiously, green superciliary color (fixed in western Mexico and nearly absent in eastern Mexico, but also present in some Central American and South American populations), and white throat color (fixed in Mexico and northern Central America, and present again in Cauca in Colombia), occurred in a leap frog pattern of geographic variation (Remsen 1984).

Complexities in the geographic variation of bill pattern and throat color (white, blue, gray, and black) of the South American populations are illustrated in Fig. 3 and also in Haffer (1974). Both summaries are preliminary, and clearly more detailed analysis is needed. Populations of Sierra de Santa Marta, northern Yungas, and southern Yungas have fixed

unique character states in bill pattern, and those of southern Yungas and Ecuador have fixed states in throat color. However, patterns of variation within the northern Andean geographic units (Cauca Region, Eastern Andes, Magdalena Basin, and Ecuador) are complex, suggesting that a large amount of contact among populations occurs.

Patterns of geographic variation in mensural characters also were complex (shown for males only in Fig. 4). In both sexes, all characters showed significant among-population components of variation (Kruskal-Wallis tests, $n = 105$ females and 193 males, both $P < 0.05$), mostly involving irregular clinal variation. Western Mexican populations were differentiated from adjacent populations in eastern Mexico and Chiapas in bill depth, and the populations of Costa Rica and Panama were distinctive in several characters (e.g., tail and bill length) in at least one sex. Individuals from the Petén region all were small in size, particularly in bill length, suggesting that they represented immature individuals. South

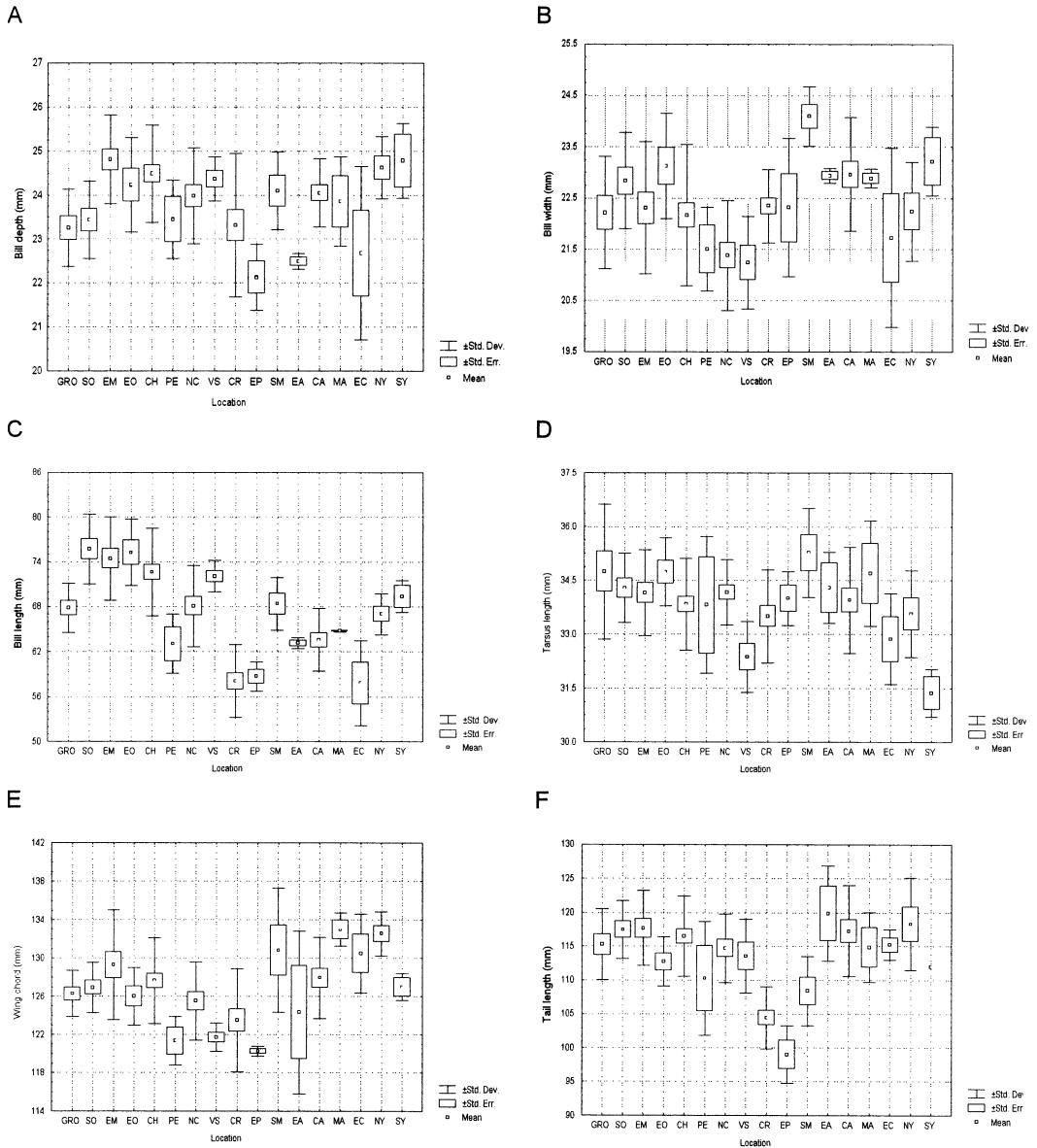


FIG. 4. Six morphometric characters (mm) for males of *Aulacorhynchus* populations. (A) Bill depth, (B) bill width, (C) bill length, (D) tarsus, (E) wing chord, and (F) tail length. Population abbreviations are given in Figure 2.

American populations showed similar patterns of irregular variation. Populations from the Sierra de Santa Marta are strikingly differentiated from the adjacent populations in most mensural characters (e.g., bill and wing length), and similar morphometric breaks are found between birds of southern Yungas and Ecuador and the neighboring areas.

DISCUSSION

Bill length.—In our examination of specimens, we were struck by the exceptional variation of bill lengths in the toucanets. Individuals in adult plumage might have a short, stubby bill as little as 62% of the length of the longest-billed individuals in the population. Frequency distributions of bill lengths

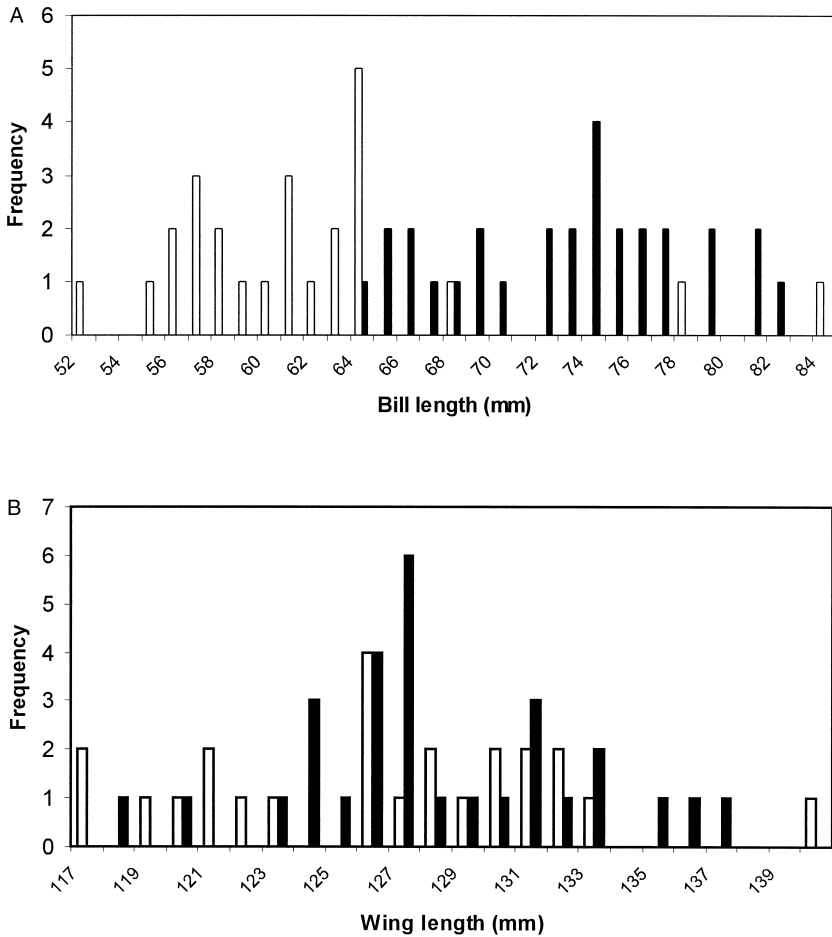


FIG. 5. Frequency of (A) bill and (B) wing lengths of female (open bars) and male (black bars) *Aulacorhynchus* toucanets from Chiapas.

for birds from one region, Chiapas (Fig. 5A), showed no clear modal point, as was seen in wing length (Fig. 5B), that could be assumed to represent individuals that had reached “adult” size. Therefore, we were led to consider the possibility of indeterminate bill growth in the toucanets.

Obviously, some limit on bill growth must exist, if only as a consequence of the unwieldy nature of such a large bill. The question is whether any substantial portion of the population lives long enough to attain that maximum bill size. We suggest that during the lifespans of most individuals in a population of toucanets, growth of the bill may well be continuous and effectively indeterminate. We know of no other characters exhibiting such

growth patterns in birds. Thus, we present this possibility in toucanets as an opportunity for further investigations, for which long term study of marked individuals would be necessary.

Lowland populations.—The populations of the lowlands of the Petén (subspecies *virescens*, in part) were peculiar in the overall small body size (in spite of adult plumage) of all ten individuals examined. Lowland populations of toucanets are sparse at best, as shown by the scarcity of records from the region (Beavers 1992). The species is listed as uncommon in the Petén in general (Howell and Webb 1995) and in the Guatemalan portion in particular (Land 1970). Russell (1964) stated that “This species is very uncommon

in British Honduras [= Belize]. . . I presume that the Emerald Toucanet is a resident, but I know of no records in the Colony from early September through January.” Based on the uniformly small size of these individuals and the propensity of immature individuals of many taxa to wander (e.g., Peterson 1991), we raise the possibility that these individuals may not represent permanent breeding populations, but rather might be young adults wandering from nearby montane regions. They certainly merit careful study to understand their reduced size.

Reconsideration of the nature of other lowland *Aulacorhynchus* populations, such as those described as the subspecies *A. p. dimidiatus* in eastern Peru, may well be in order. In their account of the rediscovery of *A. p. dimidiatus*, O’Neill and Gardner (1974) emphasized the small body size of the lowland populations, as this character also was the principal differentiation among these populations and the adjacent *A. p. atrogularis* of the eastern slope of the Peruvian Andes and adjacent Bolivia (Haffer 1974). Blake (1941), describing a low elevation *Aulacorhynchus* population in Guyana as *A. derbianus osgoodi*, also emphasized the small size of the individuals of that population. Although both descriptions mentioned characters of coloration and structure as well, we suggest that lowland *Aulacorhynchus* populations either represent wandering (and occasionally breeding) immature individuals or a fascinating repeated pattern of the evolution of dwarfism in lowland invasions.

Species limits.—The question that initiated this study was the status of the western Mexican form *A. p. wagleri*. Populations of this taxon are found from the Sierra de Atoyac of central Guerrero (possibly the coastal mountains of southwestern Michoacán as well, but these reports require confirmation and specimen documentation) south and east through the Sierra de Yucuñacua and Sierra de Miahuatlán of southern Oaxaca. Recent explorations (A.T.P. unpubl. data) in areas of possible contact with the eastern Mexican *A. p. prasinus*, i.e., the Sierra Espinazo del Diablo, Sierra de Tres Picos, and Cerro Piedra Larga of eastern Oaxaca, have detected the presence of only *prasinus*, replaced by *wagleri* in the Sierra de Miahuatlán. Thus, *wagleri* and *prasi-*

nus are everywhere allopatric. The other distinctive forms, *caeruleogularis* of Costa Rica and western Panama and *cognatus* of eastern Panama and adjacent Colombia (Hilty and Brown 1986), are similarly allopatric from populations farther north or south. Thus, nowhere in Mesoamerica is a test of sympatry of differentiated populations available, and decisions based on the Biological Species Concept (BSC) are therefore difficult.

In terms of the Phylogenetic Species Concept (PSC) and Evolutionary Species Concept (ESC), the status of these forms is not in doubt (see especially Fig. 3). Each subunit of the Emerald Toucanet complex is easily diagnosable (PSC), and independent evolutionary trajectories, with fixation of novel character states, appear to have been established (ESC). A taxonomy under these concepts would recognize four species: *A. wagleri*, an endemic of southwestern Mexico; *A. prasinus* of eastern Mexico and northern Central America [including subspecies *prasinus*, *virescens*, *stenorhabdus*, *volcanius*, and *chiapensis* of Peters (1948)]; *A. caeruleogularis* in the Cordillera Central Costa Rica and western Panama [including subspecies *caeruleogularis* and *maxillaris* of Peters (1948)]; and *A. cognatus* in the isolated mountains of eastern Panama and adjacent Colombia (Robbins et al. 1985, Hilty and Brown 1986).

Doubtless, several forms would need to be recognized as species in the extremely geographically variable northern South American populations of this complex (Haffer 1974), herein *A. albivitta* as the oldest available name, and deeper parallel analyses are needed to clarify the taxonomy of the southern populations. (Note that the application of the names *A. albivitta* and *A. atrogularis* depends on the extent of the species level taxon in which these forms are placed. These names would have priority over the adjacent, and likely conspecific forms.) Our preliminary analyses, based on morphology, suggest that the following species should be recognized in the region: *A. lautus* from the Sierra de Santa Marta, Colombia; *A. albivitta* from the eastern Andes [including subspecies *albivitta*, *griseigularis*, and *phaeolaemus* of Peters (1948)]; and *A. atrogularis* (preliminarily including the subspecies *dimidiatus*, *cyanolaemus*, and *atrogularis*).

The populations of South America afford otherwise unavailable opportunities for study of interactions between differentiated toucanet populations. Along the eastern slope of the Andes in central Ecuador, the distinctive forms *albivitta* (white-throated) and *cyanolaemus* (blue-throated) meet in what must be a fairly narrow contact zone (<100 km; M.B. Robbins pers. comm.). Montane forests in this area are essentially continuous, so populations would almost certainly be in contact. As another example, the black-throated form *atrogularis* of southeastern Peru contacts the blue-gray-throated northern form, *cyanolaemus*, and specimens from the same locality include individuals that unmistakably belong to one or the other form (Peru, Chaupe; series at AMNH). However, limited intergradation exists between both forms, as suggested by bill coloration patterns (Haffer 1974: Fig. 16.8). Study of contact zones between such different forms would be extremely helpful in evaluating the appropriateness of the taxonomic recommendations made herein.

In regard to the BSC, however, the challenge is to guess whether the differences among populations are likely to be of importance in species recognition and reproductive decisions of the toucanets. Haffer (1974) pointed out that sympatric toucanet species are in some areas very distinctive from one another, but in other areas very similar. However, bill and facial coloration are clearly important in the social and breeding behavior of toucans in general (Haffer 1974, Skutch 1967), suggesting that such characters may figure in reproductive decisions. Vocalizations also are similar throughout the geographic range of the complex, although very simple (Haffer 1974, Fjeldså and Krabbe 1990). However, distinctive allopatric populations often have very similar voices [e.g., *A. sulcatus* and *A. prasinus* in Colombia (Hilty and Brown 1986)], whereas sympatric species tend to differ greatly [e.g., *Ramphastos sulfuratus* and *R. swainsonii* in Panama (Ridgely and Gwynne 1989)]. Thus, we suggest that the populations of western Mexico, Costa Rica and western Panama, and eastern Panama, all of which are differentiated in features of bill and head coloration, may prove reproductively isolated should they come into contact, and that the four Mesoamerican forms (*wagleri*,

prasinus, *caeruleogularis*, and *cognatus*) also should be considered separate biological species. Further research also is needed to clarify the taxonomic status of the recently described form *warneri* from Los Tuxtlas (Winker 2000).

Our studies of the Mesoamerican toucanets led to more questions than they answered, and for that reason, the most appropriate conclusion to this contribution is to present topics that represent fruitful areas for further investigation. First, careful documentation of patterns of geographic variation among South American *Aulacorhynchus* populations is critical, as it is for many bird taxa of large distributional areas in the Neotropics [e.g., *Momotus momota* (Ibáñez 2000)]. Because variation is so complex and specimens so scarce, additional field collections or documentation of live birds will be necessary to make delineation of patterns possible. Study of these populations using both traditional morphological and coloration characters, as well as genetic information, would be most informative.

Finally, the geographic patterns of differentiation shown in Mesoamerican *Aulacorhynchus* populations are strikingly similar to those exhibited by the woodnymph hummingbirds of the genus *Thalurania* (Escalante and Peterson 1992) and the Bush-tanagers of the genus *Chlorospingus* (Sánchez-González 1999). Each complex shows breaks in character distributions between populations in eastern and western Mexico, northern and southern Central America, and eastern and western Panama. These coincident changes may well indicate coincident patterns of historical isolation and connection of populations. Phylogenetic study of these species groups, as well as other geographically variable montane taxa in the region (e.g., *Gral-laria guatemalensis*, *Buarremon brunneinuchus*) would be enormously interesting.

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