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A REVIEW OF THE GENUS *MOMOTUS* (CORACIIFORMES: MOMOTIDAE) IN NORTHERN SOUTH AMERICA AND ADJACENT AREAS

Una revisión del género *Momotus* (Coraciiformes: Momotidae) en el norte de Sudamérica y áreas adyacentes

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ABSTRACT

Over the last sixty years, most of the more than 20 named taxa of the genus *Momotus* have been included in a single widespread, variable species, *Momotus momota*. In recent decades, several authors have questioned this broad species concept and suggested splitting this "*Momotus momota* complex" into two or more species. However, for want of a detailed analysis no consensus has been reached regarding which and how many species should be recognized. The present study therefore seeks to provide criteria for redefining species limits in this complex through analyses of external measurements, plumage patterns and the 'hooting' primary songs among ten focal taxa occurring in the area between Nicaragua, northern Peru, Trinidad-Tobago and Guyana. Five external measurements of bills, wings and tails were made on 512 specimens of the focal taxa and an additional 30 specimens of taxa occurring in adjacent regions; data on body masses permitted use of relative mean measurements of external dimensions to examine differences in form as well as in absolute size. A subsample of 183 specimens was scored for 14 characters of plumage pattern of the underparts, crown, pectoral "stickpin", borders of the mask and tail racquets. The focal taxa break into two groups with respect to the primary song: those in which the song consists of a single long note vs. two shorter notes. Five parameters of duration and frequency were measured on sonograms of taxa in the one-note group; these and an additional six parameters were measured on sonograms of those of the two-note group, and two-note "duet" songs of one taxon of the one-note group. Data were analyzed with t-tests, ANOVA, discriminant analysis and principal components analysis. I defined species limits in this complex on the basis of two general criteria: diagnosability and the probability that the differences observed would assure maintenance of reproductive isolation should currently allopatric groups enter into contact. My results support recognition of five species-level taxa in this complex: *lessonii* Lesson 1842 (including 2-3 additional subspecies in Mexico beyond the scope of this study), *momota* Linnaeus 1766 (including the nominate, *microstephanus* Sclater 1855 and several other subspecies of eastern and southern South America beyond the scope of this study); *M. aequatorialis* Gould 1857 (including the subspecies *chlorolaemus* Berlepsch and Stolzmann 1902); *bahamensis* Swainson 1837 and *subrufescens* Sclater 1853. In the latter species I recognize as subspecies *osgoodi* Cory 1913, *argenticinctus* Sharpe 1892 and *spatha* Wetmore 1946, but find the following taxa not adequately diagnosable and recommend lumping them into nominate *subrufescens*: *conexus* Thayer & Bangs 1906, *reconditus* Nelson 1912 and *olivaresi* Hernandez & Romero 1978.

Key words: Momotidae, *Momotus momota,* morphometrics, northern South America, plumage patterns, primary songs, southern Middle America, taxonomy.

RESUMEN

A lo largo de los últimos sesenta años, la gran mayoría de los taxones del género *Momotus* se incluía en una sola especie muy variable y de amplia distribución, *Momotus momota*. En décadas recientes varios autores han cuestionado el concepto amplio de esta especie, y han hecho recomendaciones para dividir este "complejo de *Momotus momota*" en dos o más especies. Sin embargo, por falta de un análisis detallado, no existe un consenso sobre cuántas y cuáles especies deben ser reconocidas. El presente estudio intenta suministrar criterios para la definición de especies en este complejo por medio del análisis de medidas externas, patrones del plumaje y patrones del canto primario. Cinco mediciones externas fueron tomadas sobre 512 especímenes de diez taxones focales que se encuentran en el área entre Nicaragua, el N de Perú, Trinidad-Tobago y Guyana. Datos sobre la masa corporal para estos taxones permitieron el uso de medidas relativas para examinar por diferencias de forma entre taxones. Tomé, sobre una submuestra de 182 ejemplares, valores semicuantitativos de 14 caracteres de patrones del plumaje (partes inferiores, mancha pectoral, coronilla, bordes de la máscara y raquetas de la cola). Los taxones focales se dividen en dos grupos con respecto al canto primario: los en que este canto consiste en una nota larga, y los en que el canto incluye dos notas más cortas. Para los cantos de una sola nota, medí cinco parámetros de duración y frecuencia en sonogramas de tres cantos por individuo grabado; para los cantos de dos notas (incluyendo un canto de "dúo" de un taxón cuyo canto primario es de una nota), medí estos cinco parámetros de la primera nota más seis del intervalo entre notas y la segunda nota. Los datos fueron analizados con pruebas de t, ANDEVA, análisis discriminante y análisis de componentes principales. Hice la definición de los límites entre especies con base en dos criterios: diagnosticabilidad y la probabilidad de que las diferencias encontradas funcionaría en el mantenimiento de la integridad de los linajes – es decir, que favorecerían el aislamiento reproductivo si grupos actualmente alopátricos entrasen en contacto. Mis resultados apoyan el reconocimiento de cinco taxones al nivel de especies: *lessonii* Lesson 1842 (la cual incluye 2-3 subespecies adicionales de México afuera de los límites de este estudio), *momota* Linnaeus 1766 (que incluye, además de la nominal, *microstephanus* Sclater 1855 y varias subespecies más del E y S de Sudamérica más allá de los límites de este estudio); *M. aequatorialis* Gould 1857, (la cual incluye la subespecie *chlorolaemus* Berlepsch & Stolzmann 1902), *bahamensis* Swainson 1837 y *subrufescens* Sclater 1853. En esta última reconozco como subespecies válidas *osgoodi* Cory 1913, *argenticinctus* Sharpe 1892 y *spatha* Wetmore 1946, pero encuentro que los siguientes taxones no son suficientemente diagnosticables y recomiendo considerarlos sinónimos de la subespecie nominal: *conexus* Thayer & Bangs 1906, *reconditus* Nelson 1912 y *olivaresi* Hernandez & Romero 1978.

Palabras clave: Cantos primarios, Momotidae, *Momotus momota,* morfometría, norte de Sudamérica, patrones del plumaje, taxonomía, sur de Mesoamérica.

INTRODUCTION

The motmots (Family Momotidae) comprise a small group of coraciiform birds related to the todies and kingfishers. Fossils from the Oligocene of Europe and the Miocene of Florida suggest that the family originated in the northern hemisphere (Mayr 1964); the present center of diversity of the family is Middle America, where all of the genera and seven of the nine or ten currently recognized species occur today (Howell 1969). The arrival of the motmots in South America probably followed the formation of the Central American landbridge at the close of the Pliocene, ca. 3 million years ago (Snow 2000, Witt 2004).

The most diverse genus of motmots, and the only one showing extensive differentiation in South

America, is *Momotus*: in the nineteenth and early twentieth century some 25 forms were named, including ca. 20 from South America (Table 1). Ridgway (1914) and Cory (1918) recognized nine or ten species of *Momotus*. In the first comprehensive attempt to elucidate the origin and differentiation of the genus, Chapman (1923) reduced this to seven: *mexicanus, coeruleiceps, lessonii, subrufescens, momota, aequatorialis* and *bahamensis* in two main groups: "rufous-crowned" (*mexicanus*) and "blue-crowned" (the

remaining six species). However, in 1945 Peters lumped all of Chapman's "blue-crowned" group into *M. momota*, apparently following the "biogeographic species concept" developed by Hellmayr: allopatric representatives of a common stock should be considered subspecies, the "biogeographic species" so defined thus comprising all representatives of this stock. This concept of a broadly defined *M. momota* was followed, explicitly or implicitly, by nearly all subsequent authors through most of the twentieth century (e.g.,

Table 1. Nomenclatural treatments of *Momotus* taxa in major reference works from the time of their original descriptions through the Handbook of Birds of the World (Snow, 2000).

| Original description	Cory 1918	Chapman 1923	Peters 1945	Snow 2000
Ramphastos momota Linn. 1766	*Momotus m. momota*	*Momotus m. momota*	*Momotus m. momota*	*Momotus m. momota*
Momotus lessoni Lesson, 1842	*Momotus l. lessonii*	*Momotus l. lessonii*	*Momotus momota lessonii*	*Momotus m. lessonii*
Prionites bahamensis Swainson, 1837	*Momotus bahamensis*	*Momotus bahamensis*	*Momotus momota bahamensis*	*Momotus momota (?) bahamensis*
Momotus subrufescens Sclater, 1853	*Momotus s. subrufescens*	*Momotus s. subrufescens*	*Momotus momota subrufescens*	*Momotus m. subrufescens*
Momotus microstephanus Sclater, 1855	*Momotus microstephanus*	*Momotus momota microstephanus*	*Momotus momota microstephanus*	*Momotus momota microstephanus*
Momotus aequatorialis Gould, 1857	*Momotus aequatorialis aequatorialis*	*Momotus aequatorialis aequatorialis*	*Momotus momota aequatorialis*	*Momotus aequatorialis aequatorialis*
Momotus argenticinctus Sharpe, 1892	*Momotus argenticinctus*	*Momotus momota argenticinctus*	*Momotus momota argenticinctus*	*Momotus momota argenticinctus*
Momotus venezuelae Sharpe, 1892	*Momotus venezuelae venezuelae*	*Momotus subrufescens subrufescens*	*Momotus momota subrufescens*	*Momotus momota subrufescens*
Momotus aequatorialis chlorolaemus Berlepsch & Stolzman, 1902	*Momotus aequatorialis chlorolaemus*	*Momotus aequatorialis chlorolaemus*	*Momotus momota chlorolaemus*	*Momotus momota chlorolaemus*
Momotus conexus Thayer & Bangs, 1906	*Momotus subrufescens conexus*	*Momotus subrufescens conexus*	*Momotus momota conexus*	*Momotus momota conexus*
Momotus conexus reconditus Nelson, 1912	*Momotus subrufescens reconditus*	*Momotus subrufescens reconditus*	*Momotus momota reconditus*	*Momotus momota conexus*
Momotus osgoodi Cory, 1913	*Momotus venezuelae osgoodi*	*Momotus subrufescens osgoodi*	*Momotus momota osgoodi*	*Momotus momota osgoodi*
Momotus momota spatha Wetmore, 1946	(Not described)	(Not described)	(Not described)	*Momotus momota spatha*
Momotus momota olivaresi Hernández & Romero 1978	(Not described)	(Not described)	(Not described)	*Momotus momota olivaresi*

AOU 1983, 1998; Meyer de Schauensee 1948-52, 1966).

During the final decades of the century, various authors began to question the broad species concept of Peters for *M. momota,* especially with regard to the large Andean form *aequatorialis*. Parker et al. (1982) recognized *aequatorialis* as a distinct species; Fjeldså & Krabbe (1990) kept *aequatorialis* in *momota* but stated that it "almost certainly represents a distinct species or allospecies". Stotz et al. (1996) gave *aequatorialis* separate treatment under *momota*, and Ridgely & Greenfield (2001) and Snow (2000) explicitly recognized it as a separate species, mentioning morphological, vocal and altitudinal differences from *momota* but not specifying or describing these in detail. However, the South American Checklist Committee of the AOU rejected a proposal to recognize *aequatorialis* as a species because of insufficient published information justifying this split, and because probably other species should be recognized within the broad *M. momota* as well, such that any taxonomic decision should await the publication of a more comprehensive evaluation of at least the South American forms (Remsen et al. 2009). I therefore decided to undertake this task.

My own interest in motmots had been stimulated by the seemingly "hard-wired" behavior of the motmots visiting my backyard bird feeder in Costa Rica, where birds would habitually beat and "kill" pieces of bread before consuming them; it was several months before they appeared to learn that this procedure was unnecessary. Upon arriving in Colombia, I was amazed at hearing the vocalizations of motmots in the northern Chocó, which sounded totally different from the birds I had heard for years in Costa Rica (I was later bemused to learn that recordings of the Chocó birds that I sent to J. W. Hardy for archiving were labeled "probably misidentified"). This convinced me that vocalizations in such "hard-wired" birds were likely innate, and would therefore be useful taxonomic characters. Further field experience with motmots in eastern Colombia and the Central Andes, with different vocalizations in each case, suggested to me that at least three species-level taxa might occur in the country. Colombia therefore represented an appropriate area in which

to center a taxonomic revision of the "*Momotus momota* complex". However, I soon found that to determine the affinities of several problematic taxa and resolve questions of nomenclature, I would have to expand the study to several adjacent countries. The objective of this study is therefore to analyze external measurements, plumage patterns and vocalizations of all recognized forms from southern Central America and northern South America to evaluate the species and subspecies taxonomy of this part of the complex.

THE FORMS OF *MOMOTUS* INHABITING NORTHERN SOUTH AMERICA AND ADJACENT AREAS.- The last comprehensive review of the forms of the *M. momota* complex over this area was that of Chapman (1923), although Snow (2000) discussed briefly the forms usually recognized in recent years. Here I review the subspecies recognized in the area between Nicaragua and N Peru and extreme W Brazil to Guyana, including Trinidad and Tobago (Table 1; Fig. 1); this area includes the ranges of nearly all of Chapman's species as well as of my own personal field experience. Because all authorities to date agree that the motmots, and specifically the genus *Momotus,* probably originated in tropical North or Middle America (Chapman 1923, Mayr 1964, Snow 2000), I begin with the medium-sized, variably colored *M. m. lessonii*, which occurs from extreme southern Mexico to southwestern Panama. A gap of at least 300 km separates the range of this form from that of the much smaller and somewhat differently patterned *M. m. conexus* of central and eastern Panama, which also shows considerable individual variation in the coloration of the underparts. In extreme eastern Darién and adjacent northwestern Colombia *conexus* is replaced by the similar but generally more intensely colored *reconditus*. Considering the degree of individual variation in coloration of both forms, Wetmore (1965) considered that *reconditus* was not reliably distinguishable from *conexus* and lumped the two under the older name *conexus*. In turn, *conexus* (or *reconditus*, if recognized) intergrades over a rather broad area of northwestern Colombia with the slightly paler *M. m. subrufescens* of similar pattern. As currently defined, the range of *subrufescens* extends from the Santa Marta region southwards through the length of the Magdalena valley of
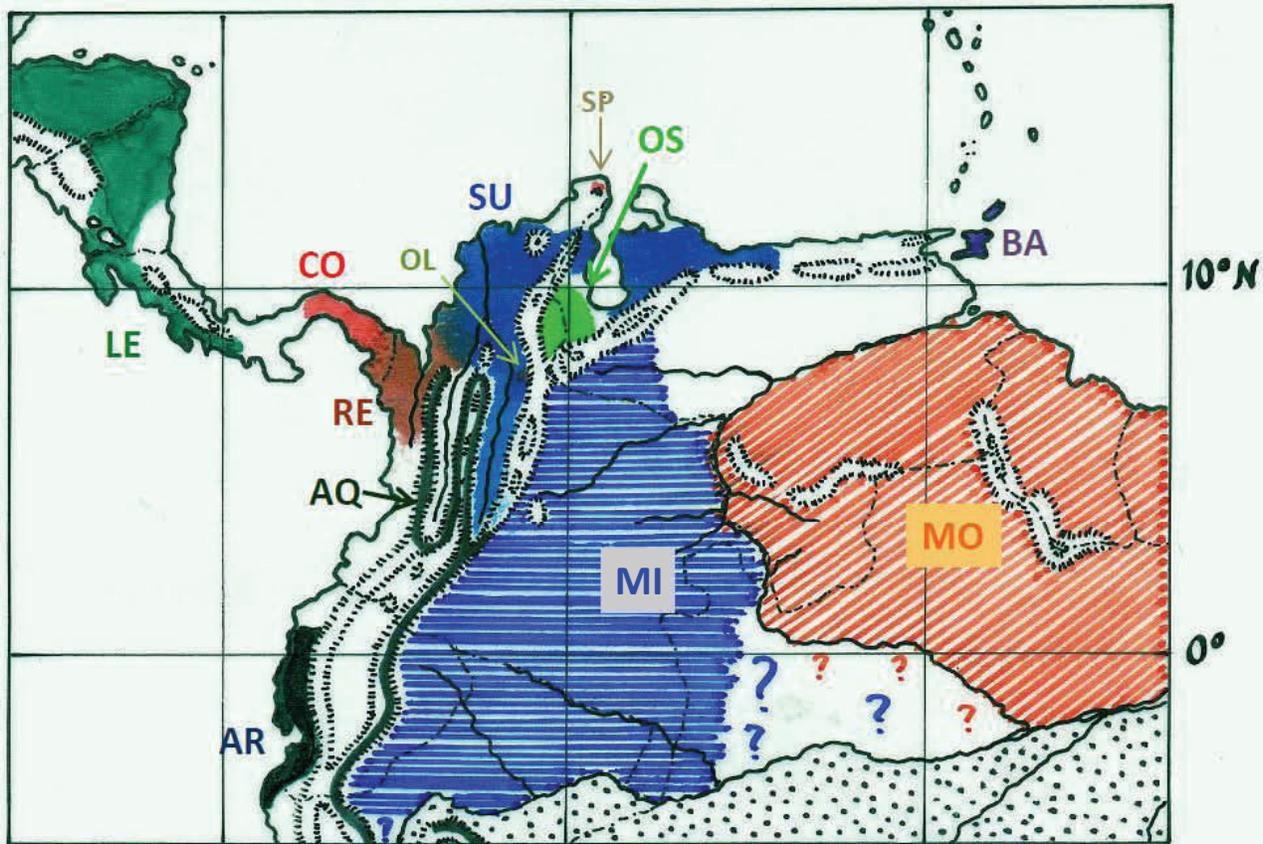
Figure 1. Distributions of the forms of the "*Momotus momota*" complex treated in this study: From northwest to southeast, LE = *lessonii*; CO = *conexus*; RE = *reconditus*; SU = *subrufescens*; OL = *olivaresi*; SP = *spatha;* OS = *osgoodi*; BA = *bahamensis*; AQ = *aequatorialis*; AR = *argenticinctus*; MI = *microstephanus*; MO = *momota*. Note the high degree of geographical replacement among taxa; only *conexus*, *reconditus* and *subrufescens* overlap appreciably (and *olivaresi* is indistinguishable from *subrufescens*).

central Colombia and eastward along the coastal district of northern Venezuela (the latter populations were once considered to represent the subspecies *venezuelae*, long since synonymized with *subrufescens*).   Within *subrufescens,* the Magdalena valley population averages slightly darker overall, and in fact is virtually indistinguishable in this respect from *conexus* of Panama; it was previously assigned to that form, although separated from it by the still darker *reconditus*. The population of the dry Chicamocha valley, a tributary of the Magdalena, was separated as the subspecies *olivaresi* by Hernández & Romero (1978). Isolated in the moist Serranía de Macuira at the tip of the desertic Guajira Peninsula of extreme N Colombia is *spatha*, described by Wetmore (1946); it is similar in size and pattern to *subrufescens* but is much paler. Apparently also isolated from *subrufescens* in the lowlands and adjacent slopes south of the Lago de Maracaibo in

extreme NE Colombia and NW Venezuela is the very rufescent race *osgoodi*, which is also similar in size.   Another isolated and still more deeply rufescent form is *bahamensis* of Trinidad and Tobago; it is also appreciably larger than *subrufescens* and *osgoodi* and Snow (2000) noted that it may represent a separate species.

The eastern lowlands of Colombia, from the Llanos to the Amazon, are almost entirely occupied by the medium-sized *M. m. microstephanus*, which also occurs throughout eastern Ecuador and adjacent northeastern Peru and (probably) western Brazil (an area very poorly collected). Only in the extreme northeast along the Orinoco may there be intergradation with the considerably larger subspecies *momota* of southern Venezuela and the Guianas, which ranges south to the north bank of the Amazon.   Several other races occupy the Amazon basin further to the east and south, but

because none approach closely the area considered here, they will not be discussed further. A notably problematic form isolated west of the Andes in southern Ecuador and northern Peru is *argenticinctus*, which in its small size and overall plumage pattern resembles a very green member of the *subrufescens* group, although some aspects of its crown pattern approach *microstephanus* or *aequatorialis*. In fact, Chapman (1923) included it in his *momota* group, otherwise restricted to the lowlands east of the Andes, on the basis of its close resemblance to the form of *momota* inhabiting the southernmost part of the species range in Bolivia, southern Brazil and Paraguay. I present reasons below for considering this resemblance to represent homoplasy and that the affinities of *argenticinctus* lie with *subrufescens* and its allies.

The final member of the *M. momota* complex occurring in Colombia is the large, green highland form *aequatorialis*, which occurs widely in the Western and Central Andes of Colombia but occupies the Eastern Andes only at their southern terminus in Cauca and extreme SW Caquetá. Its range extends south mainly along the eastern slope of the Andes of Ecuador and extreme northern Peru, and the very similar but even greener *chlorolaemus* replaces it in the Andes of eastern Peru. As mentioned above, *aequatorialis* (with *chlorolaemus*) is the form several authors have recognized as distinct from *M. momota,* but a detailed justification has been lacking. In addition to *aequatorialis*, Snow (2000) recognized two "groups of races" of *M. momota* in South America: a "*subrufescens* group" including *conexus* (with *reconditus*), *subrufescens*, *osgoodi* and *bahamensis*; and a "*momota* group" for all the other races, including *argenticinctus* and (somewhat surprisingly) *olivaresi*; this arrangement was also followed by Restall et al. (2006). This summary makes it clear that a number of taxonomic problems remain to be resolved among the forms of the "*Momotus momota* complex" inhabiting the area between southern Middle America and northern South America, which I propose to address in the present study.

METHODS AND MATERIALS

For measurements and plumage descriptions, I examined study skins in the following museums: the American Museum of Natural History, the Field Museum of Natural History and the Academy of Natural Sciences of Philadelphia in the USA, and the Instituto de Ciencias Naturales of the Universidad Nacional de Colombia (Bogotá), the Museo de la Universidad de La Salle (Bogotá) and the Instituto Alexander von Humboldt (Villa de Leyva) in Colombia. In addition, Claudia Rodríguez and Kristof Zyskowski measured a number of specimens in the U.S. National Museum and the Peabody Museum of Yale University, respectively. In all, I analyzed measurements of 512 specimens of ten "focal" taxa (from north to south and west to east): *lessonii* (Nicaragua, Costa Rica), *conexus* (Panama), *reconditus* (Panama, Colombia), *subrufescens* (Colombia), *osgoodi* (Colombia, Venezuela), *argenticinctus* (Ecuador, Peru), *bahamensis* (Trinidad and Tobago), *microstephanus* (Colombia), *momota* (Venezuela) and *aequatorialis* (Colombia). I also measured smaller samples (10-12 each) of *subrufescens* from N Venezuela and *microstephanus* and *aequatorialis* from Ecuador to check for geographic variation within these taxa, as well as 10 specimens of *chlorolaemus* from Peru and two specimens of the seldom-collected *spatha* from extreme N Colombia. I obtained body masses of motmots from various sources (see acknowledgments).

PATTERN AND COLORATION OF PLUMAGE.- Great individual variation in the overall tone of the plumage, from green to rusty or rufescent tones, exists among the specimens of many forms of *Momotus* (Ridgway 1911, Chapman 1923). A number of subspecies and species have been named on the basis of such variation and subsequently synonymized. For this reason, I decided to focus not on the overall coloration but rather on the plumage pattern: the relative distribution of greener vs. rustier tones on the underparts and the details of color and pattern of the crown, mask and tail. I thus discovered a number of taxonomically useful characters (Fig. 2, Table 2). Few characters provided absolute distinctions, but average differences in many features were clearly evident. Hence, for each of the 14 characters chosen I ranked the plumage of a specimen from 0 to 2, 3 or 4 depending upon the character in question (Table 2).

Table 2. Scoring of plumage characters used in comparisons between different forms of the *Momotus momota* complex in Colombia and adjacent areas (see also Fig. 2).

Character 1: distribution of greenish or tawny to rufescent tones of the underparts
  Scores: 0 = chest decidedly greener than belly
         1 = chest slightly greener than belly
         2 = chest and belly very similar in hue
         3 = chest slightly more rufescent or tawny than belly
         4 = chest much more rufescent or tawny than belly
Character 2a: color of the thighs (tibial feathering)
  Scores: 0 = blue-green
         1 = green
         2 = olive green
         3 = tawny olive
         4 = tawny or rufescent
Character 2b: color of the flanks and abdomen, adjacent to the thighs
  Scores: the identical scores were used as for Character 2a: I combine these characters to analyze the difference between them: the degree of contrast between the color of the thighs and that of adjacent ventral areas.
Character 3: number of black feathers in the "stickpin" of the breast (only specimens in adult plumage, with no detectable molt): numbers vary from 1 to 5.
Character 4: extent of turquoise borders on longer feathers of the "stickpin"
  Scores: 0 = no turquoise border
         1 = border narrow, covering less than half of the feather margin
         2 = border narrow but covering half or more of the feather margins
         3 = border broad, conspicuous and occupying over half of the feather margin
Character 5: color of the anterior portion of the diadem
  Scores: 0 = anterior diadem entirely sky-blue to turquoise
         1 = clay-color or brownish in the feather bases of the anterior diadem
         2 = clay-color or rufescent tones evident in the medial anterior diadem
         3 = clay-color or rufous conspicuous, covering much or all of the medial portion of the anterior diadem and diffusing to lateral portions
Character 6: color of the posterior portion of the diadem
  Scores: 0 = entirely blue
         1 = mostly blue with some violet along posterior border
         2 = posterior diadem blue anteriorly, violet posteriorly in about equal proportions
         3 = posterior diadem mostly violet, inner border blue
         4 = entirely violet
Character 7: relative widths of anterior and posterior portions of the diadem
  Scores: 0 = anterior portion wider
         1 = anterior and posterior portions about the same width
         2 = posterior portion wider
Character 8: presence of a black border separating posterior diadem from nape
  Scores: 0 = black border absent
         1 = black border narrow, discontinuous, inconspicuous
         2 = black border complete, broader, conspicuous
Character 9: degree of development of the upper posterior border (A) of the mask
**Character 10:** degree of development of the anterior lower (malar, B_1) border of the mask
Character 11: degree of development of the middle lower (suborbital, B_2) border of the mask
Character 12: degree of development of the posterior lower border (B_3) of the mask
  Scores: 0 = no bright feathers (turquoise or violet) in border
         1 = border inconspicuous, bright feathers few and scattered
         2 = border conspicuous, bright feathers form a solid band along the black (these scores apply to characters 9-12)
Character 13: presence and extent of a rufous area on the occiput and nape
  Scores: 0 = no rufous present
         1 = rufous present but wholly concealed beneath feathers of posterior diadem
         2 = a small, inconspicuous area of rufous visible on occiput
         3 = rufous on occiput conspicuous and extensive, spreading onto nape
Charcter 14: pattern of blue and black on tail racquets
  Scores: 0 = racquet entirely blue, no black
         1 = blue with indistinct dusky to black border covering < ¼ of racquet
         2 = blue basally, distal ¼ - ½ black
   3 = blue basally, black distally covering more than ½ of racquet
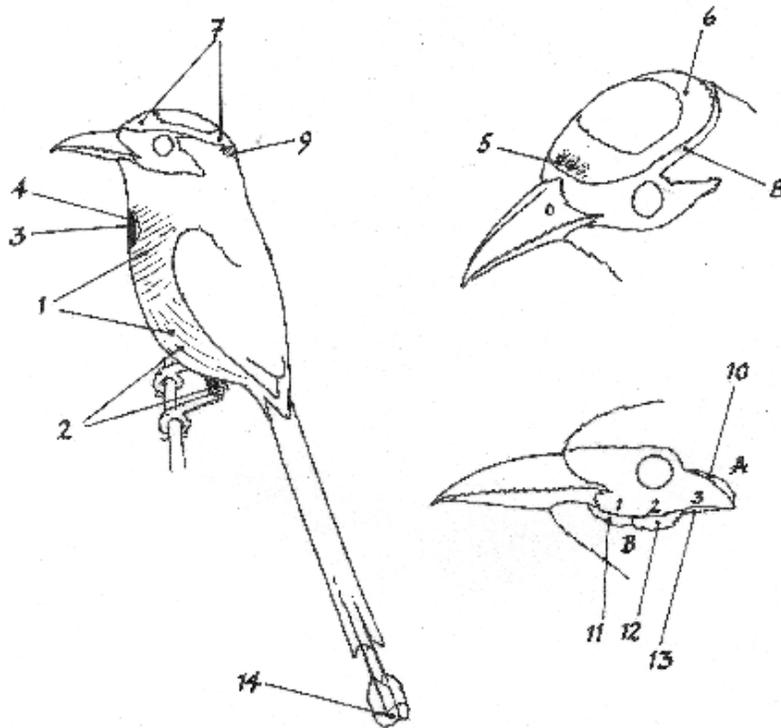
Figure 2. Summary of characters of plumage pattern useful for distinguishing between taxa of the "*Momotus momota* complex". 1: color contrast between chest and abdomen; 2: color contrast between thighs and flanks; 3: number of black feathers, and 4: extent of blue borders, on the "stickpin" of the center of the breast; 5: the extent of brown or rufous in the feathers of the anterior diadem; 6: relative extent of blue vs. violet in the posterior diadem; 7: relative widths of anterior vs. posterior segments of diadem; 8: presence and extent of black posterior border of the diadem; 9: presence and extent of rufous on nape or occiput; 10: extent of pale border to auricular portion of mask; 11, 12, 13: extent of pale borders to anterior, middle and posterior portions of lower edge of mask; and 14: extent of black tip to tail racquets. For how these characters were scored, see Table 2.

EXTERNAL MORPHOLOGY.- The following measurements were taken with dial calipers on all specimens to the nearest 0.1mm: length of exposed and total culmen, length of bill from the anterior edge of the nostril, height of bill at nostril and chord of the closed wing. Tail length including the racquets was taken to the nearest 0.5mm with a thin metal ruler. Sample sizes for the different measurements varied somewhat because the bills of a number of specimens had been damaged by shot, whereas some others had been prepared with the beak open or with a plug of cotton in the mouth that affected the measurement of bill height; a considerable number of specimens had the tips of the tail damaged (racquets broken or very worn) or were molting the rectrices. I obtained body masses of a number of mist-netted motmots of several taxa, and several other observers and organizations kindly supplied many additional weights. Sample sizes for body masses were usually much smaller than for measurements and masses were available for only a few of the specimens measured. Because a considerable number of specimens and virtually all birds weighed in the field were unsexed, I calculated the mean mass of all birds of a given taxon without regard for sex.

VOCAL CHARACTERS.- For these analyses I considered only the single or double hoot (the presumed primary "song"), from which the name *Momotus* comes. Although motmots possess a variety of other calls, none have been recorded consistently in all of the forms considered here, making it difficult or impossible to establish homologies for comparative analyses. Recordings were obtained from a number of sources (see Acknowledgments and Appendix 1) and sonograms were produced using Raven and Syrinx software, as well as with a Kaye Elemetrics sonograph. When possible, I analyzed three successive hoots for at least three individuals per taxon from sonograms; however, for several taxa recordings of only two individuals were available. The following temporal parameters were measured in milliseconds for each "song": a) length of the first note; b) length of the initial ascending portion of the first note; c) length of the interval between the first and second notes; d) length of the second note; and e) length of the ascending portion of the second note. When the song consisted of only a single note or hoot, I assigned a value of zero to parameters d-e and excluded c. In addition, I measured the initial, peak and final frequencies of the first and second hoots

2-note songs   **1-note songs**
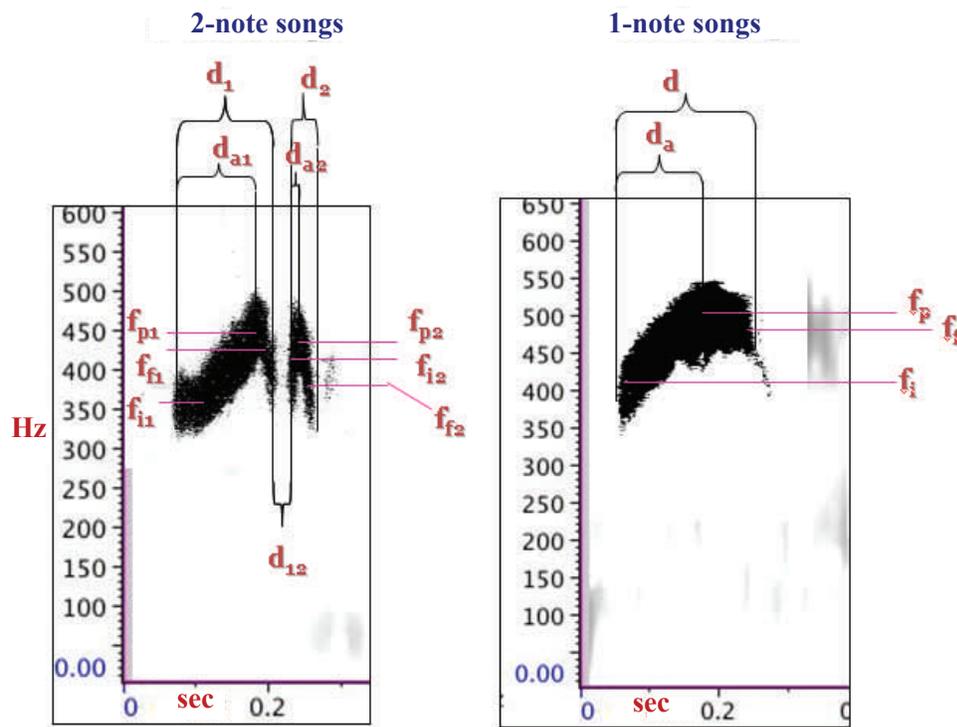
Figure 3. Temporal and frequency parameters measured in one- and two-note primary songs of members of the *Momotus momota* complex. **d**=duration (in milliseconds or seconds) **f**=frequency (in Hz). d_a=duration of the initial ascending portion of a note; f_i=initial, f_p=peak and f_f=final frequency of a note.

in Hz (see Fig. 3 for a summary of these measurements). I also calculated the following ratios: length second note:length first note; length internote interval:length first note; peak:initial frequencies and final:initial frequencies of the first and (where present) second notes, and peak frequencies of second:first notes.

STATISTICAL ANALYSES.- For comparing plumage patterns between taxa, I conducted a discriminant analysis with the Statgraphics 5.1 statistical package, using samples of 10 to 30 individuals of each taxon. These samples included approximately equal numbers of males and females; in no species did I find any evidence for sex differences in plumage color or pattern. Sample sizes for this analysis were smaller than for those comparing external measurements, because a number of characters were discovered while measuring and examining specimens in the course of the study; only individuals for which all 14 characters had been scored were included (N = 183). A principal components analysis (PCA) was conducted using the mean values for each plumage character (from Appendices 3-10) with the PAST3 statistical package.

I examined sexual dimorphism for each external measurement by comparing means of males and females of each taxon with Student´s t-tests, using the Bonferroni correction to establish α. I compared means of all measurements for all taxa using one-way ANOVA with the Bonferroni correction for *a posteriori* analyses using the Statistix 7 package, and with PCA using the PAST3 package. I removed the effects of differences in absolute size in order to compare relative lengths of structures (shape parameters) by dividing the means of all linear measurements by the cube root of the mean body mass for each taxon (cf. Stiles et al. 2005). Use of taxon means was necessary because the birds weighed were in nearly all cases different from the specimens measured. I used PCA to compare these relative means.

I also used PCA to compare the means of the various measurements of the primary song of the different taxa. Use of means was required because of small sample sizes for several taxa. I expressed frequency variables in Hz and applied a correlation-based model of PCA because two different variable types were being included (durations and frequencies). I found that in taxa for which samples

of five or more songs were available, great variation often occurred among different individuals in the frequency or pitch of their songs. When different individuals are countersinging, one also frequently hears considerable variation in pitch between their songs; although it is sometimes stated that the females sing higher-pitched songs, definite proof of this is lacking. Hence, for some PCA I included frequencies for particular song parameters, whereas in others I removed the effect of absolute frequency by comparing ratios of frequencies of particular parts of the song (e. g., ratio of initial to peak frequencies of note 1; ratio of peak frequencies of notes 1 and 2, etc).

RESULTS

Comparisons of plumage pattern

In the absence of detailed descriptions of the plumages of most taxa, particularly with respect to the degree of individual variation in color and pattern, I present such descriptions for each of the ten "focal" forms treated here in Appendix 2, emphasizing the areas that present taxonomically useful variations (see Fig. 2, Table 2). The taxonomic validity of these forms will be analyzed and discussed beyond. Quantitative comparisons of these features are given in Appendices 3 through 10. In the comparisons that follow, I discuss the values for each taxon of the birds scored on the semiquantitative scales of plumage coloration (Table 2).

DISTRIBUTION OF COLORS ON CHEST VS. ABDOMEN (character 1, Appendix 3): Although the absolute degree of greenness vs. rustiness showed individual variation in all forms, the taxa treated here fell into two main groups with respect to the hues of the chest vs. the abdomen. In *conexus, reconditus, subrufescens* and *argenticinctus* (and *spatha*), the chest was decidedly greener or more olivaceous than the abdomen, which was more ochraceous to rusty. In *osgoodi* and *bahamensis*, the chest and abdomen were more nearly concolorous: in both, the underparts were more uniformly rufous with a usually slight greenish wash across the chest (in a few *osgoodi*, this was more conspicuous and rather resembled the condition in *reconditus*). However, both of these agreed with the preceding forms in

that where a difference existed, the chest was greener than the abdomen. The opposite was true in *lessonii, microstephanus, momota* and *aequatorialis*, in which the abdomen was slightly to decidedly greener than the chest (Figs. 4 and 5).

COLOR OF THIGHS VS. FLANKS AND ABDOMEN (character 2, Appendix 4): *Bahamensis* differed from all other forms in its much more bluish-green thighs; the thighs of *aequatorialis, lessonii, microstephanus, momota* and *argenticinctus* were usually green whereas those of *conexus, reconditus, subrufescens* and *osgoodi* were decidedly more olive. The contrast between thighs and abdomen was very strong in *bahamensis*, moderate in *conexus, reconditus, subrufescens, argenticinctus* and *osgoodi*, slight in *microstephanus* and *momota*, and virtually nonexistent in *lessonii* and *aequatorialis*.

SIZE AND COLORS OF THE PECTORAL "STICKPIN" (Appendix 5): The mean number of black feathers in the pectoral spot (character 3) varied rather little among taxa, being greatest in *aequatorialis* and *argenticinctus*, intermediate in *momota* and *microstephanus,* and lowest in the remaining forms. The turquoise borders on the longest black feathers (character 4) were broadest and most conspicuous in *bahamensis*, moderately so in *conexus, reconditus, subrufescens, osgoodi* and *argenticinctus*, less so in *microstephanus* and *momota,* and least developed in *lessonii* and *aequatorialis* (see Figs. 4 and 5).

FORM AND COLORS OF THE DIADEM (Appendices 6,7; see Fig. 6): The presence of brown, clay-color or rufous mixed in with the blue or turquoise of the medial anterior diadem was a conspicuous feature in many individuals of *conexus, reconditus, subrufescens, osgoodi, argenticinctus* and especially *bahamensis*. The blue of this portion of the diadem in these taxa also tended toward a silvery-turquoise hue. In all other forms the anterior diadem was purer sky-blue, with brownish shades very inconspicuous as in *microstephanus* and *momota*, or essentially lacking as in *lessonii* and *aequatorialis* (character 5). The posterior portion of the diadem of *aequatorialis* was usually entirely blue, at most with a small amount of violet peripherally; blue and violet were present in fairly
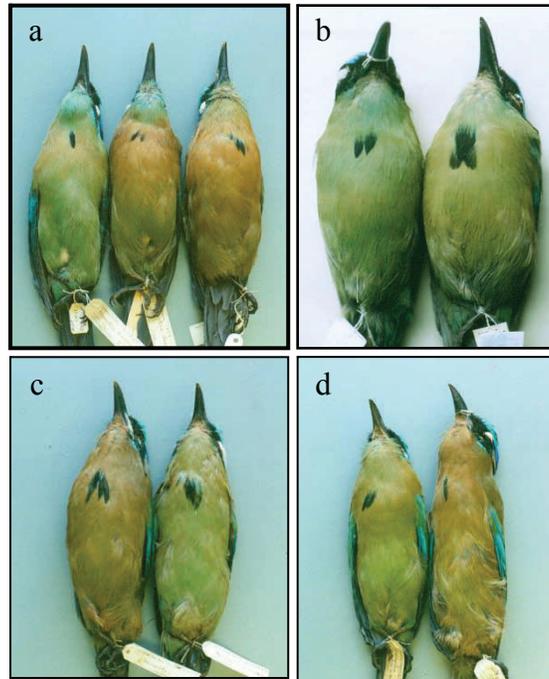
Figure 4. Variation in ventral coloration in four taxa of the "*Momotus momota* complex". **a.** *lessonii*; **b.** *aequatorialis*; **c.** *microstephanus*; and **d.** *momota.* Note the high degree of variation in *lessonii*; at the other extreme is *aequatorialis,* which is always quite green; *momota* and *microstephanus* are intermediate.
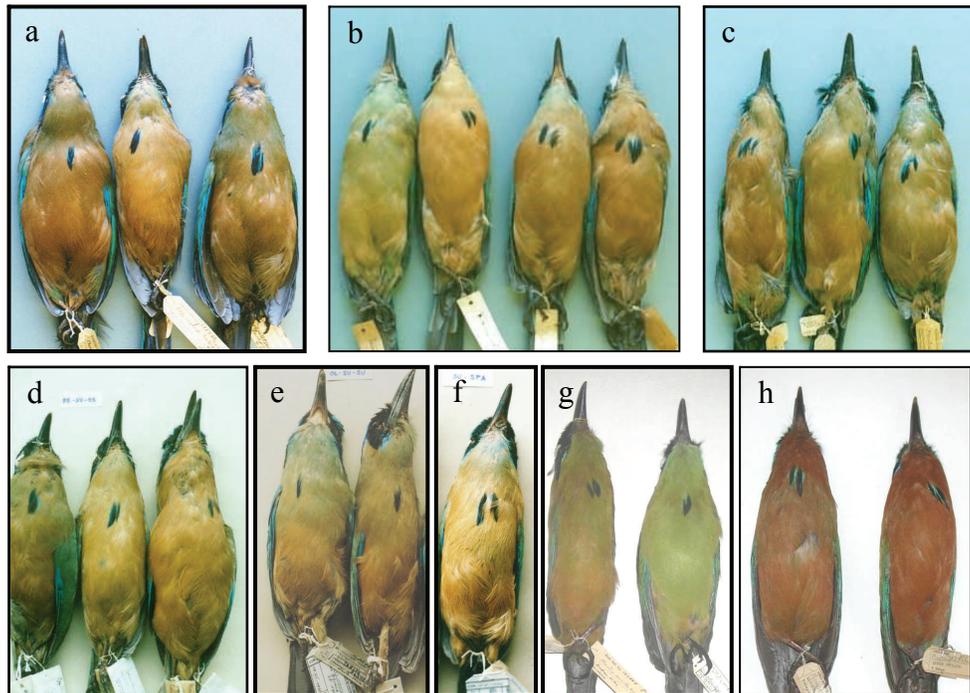
Figure 5. Ventral coloration in the "*subrufescens* group". Note that in all taxa, the chest is as green or greener than the abdomen. **a.** three specimens of *conexus*; **b.** four specimens of *subrufescens* from Bonda, Dept. of Magdalena, N Colombia, showing the degree of variation frequent in taxa of this group; **c.** three specimens of *reconditus,* which averages darker and more olivaceous than *subrufescens*; **d.** typical plumages of (left to right) *reconditus, subrufescens* and *osgoodi*; the latter more uniformly rufescent below; **e.** the type of *olivaresi* and a typical example of *subrufescens*; note similarity in size and pattern (cf. b. above); **f.** *spatha*; note pale coloration; **g.** *argenticinctus,* very rusty and very green examples; **h.** *bahamensis*; note the deeper, darker rufous coloration, nearly uniform below.
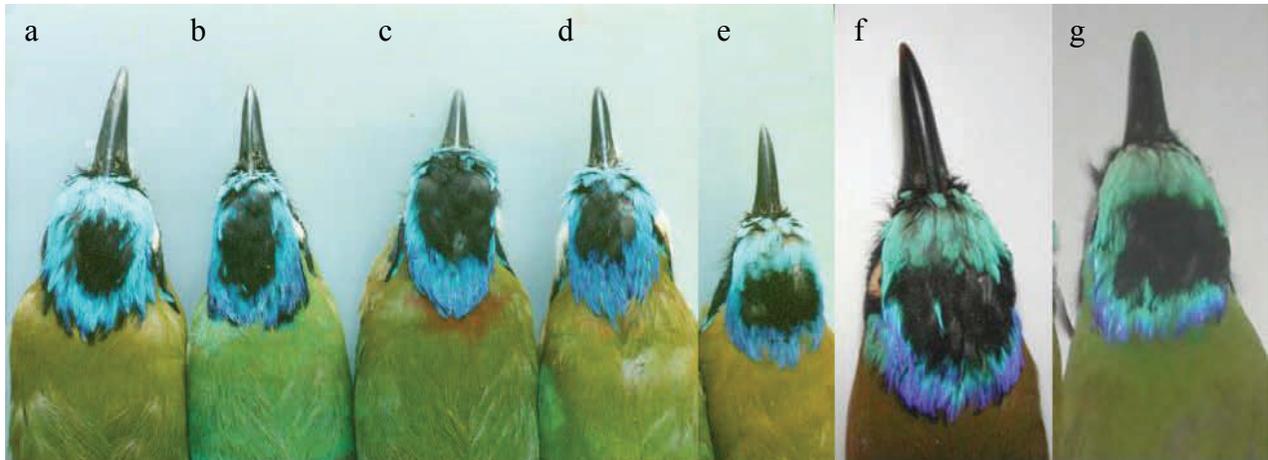
Figure 6. Crown patterns of several taxa of the *Momotus momota* complex. **a.** *aequatorialis*: note even width and uniform color all around the diadem, black posterior border; **b.** *lessonii*: similar to preceding but more violet in posterior part of diadem; **c.** *momota*: posterior part of diadem broadest; no black border; note rufous on nape; **d.** *microstephanus*: as preceding but usually only a trace of rufous on nape; **e.** *subrufescens*: anterior portion of diadem broadest and paler turquoise than lateral or posterior portions, often with brownish feather bases; **f.** *bahamensis*: pattern similar to preceding; note trace of black border and more violet in posterior portion; **g.** *argenticinctus*: overall pattern similar to preceding two forms; note how turquoise continues along interior border of diadem to encircle black crown.
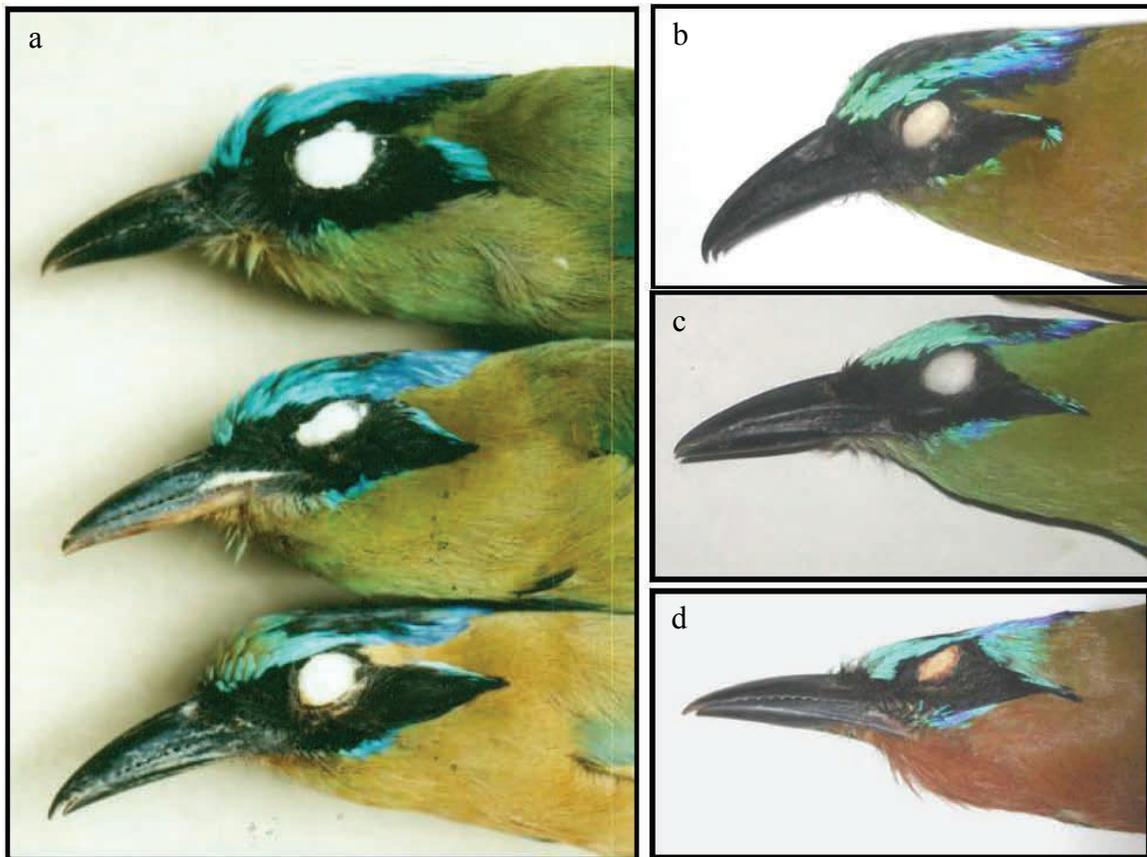
Figure 7. Masks of several taxa of the *Momotus momota* complex. **a.** top to bottom: *aequatorialis, microstephanus, subrufescens*; **b.** *lessonii*; **c.** *argenticinctus*; **d.** *bahamensis*. Note poor development of lower (B) portion of border, conspicuous upper (A) portion in *aequatorialis*; lower border (B) extending further anteriorly in *microstephanus* than in *subrufescens*; heavy black lateral and posterior border of diadem in *aequatorialis* and *lessonii*; similarity of patterns of *argenticinctus* and *subrufescens;* and diffusion of blue between mask and diadem posteriorly in *bahamensis*.

similar proportions in *lessonii* and *argenticinctus*, whereas in all other forms the violet was much more extensive, with blue present only along the inner border if at all (character 6).

A clear separation existed between *conexus, reconditus, subrufescens, osgoodi, argenticinctus* and *bahamensis*, in which the anterior portion was decidedly broader than the posterior portion, and *lessonii, microstephanus, momota* and *aequatorialis*, in which the posterior portion was similar to or broader than the anterior (character 7). A black border around the posterior diadem was broad and conspicuous in *lessonii* and *aequatorialis*, narrow and often incomplete in *bahamensis*, still narrower and nearly always incomplete and inconspicuous in *argenticinctus, microstephanus* and *momota,* and essentially absent in *conexus, reconditus, subrufescens* and *osgoodi* (character 8).

DEVELOPMENT OF THE PALE BORDER OF THE MASK (Appendix 8, Fig. 7): Segment A (character 9) of the border (see Fig. 2) was usually inconspicuous in most forms but was moderately developed in *lessonii* and conspicuous and well developed in *aequatorialis* and *bahamensis*. In the former, this area was sharply defined and pale turquoise and constituted the most conspicuous portion of the entire border; this portion of the border was bluer in *bahamensis* and the blue color tended to diffuse over much or all of the area between the mask and the diadem.

The lower border (B) of the mask was equally (*bahamensis, lessonii*) or much more strongly developed (all other forms) than the A portion, the opposite of *aequatorialis*. In *microstephanus* and *momota* the anterior (B1, character 10) and medial (B2, character 11) portions of this border were equally well developed, whereas in the other forms, the medial portion was much broader and conspicuous, constituting by far the most conspicuous part of the border in *conexus, reconditus, subrufescens, osgoodi* and *argenticinctus*. The posterior (B3, character 12) portion was poorly developed in all forms (see Appendix 8).

RUFOUS ON THE OCCIPUT AND NAPE (character 13,

Appendix 9; see Fig. 6): In this feature *momota* stood apart from all the rest in having a typically conspicuous rufous area on the nape; among the others, only *microstephanus* sometimes showed conspicuous rufous here, although this color was more often concealed or absent. In *conexus, reconditus, subrufescens, osgoodi, bahamensis* and *argenticinctus* a rufous area was usually present on the occiput but was concealed beneath the posterior portion of the diadem and rarely visible; rufous was usually lacking altogether in *lessonii* and *aequatorialis*.

COLOR AND PATTERN OF THE RACQUETS (character 14, Appendix 10, Fig. 8): The racquets were sharply bicolored blue and black in *lessonii, conexus, reconditus, subrufescens, osgoodi, bahamensis* and *argenticinctus*; the terminal half or more was usually black in all but *lessonii*, in which the black averaged less extensive. In *momota* and *microstephanus* this pattern was usually only faintly suggested in the form of a more or less indistinct dusky posterior border of the racquet, whereas in *aequatorialis* the racquet was usually uniform dark blue without any black or dusky.
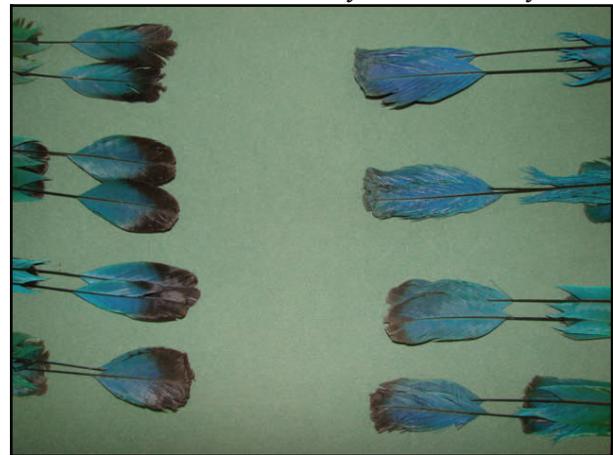
Figure 8. Racquets of several taxa of the *Momotus momota* complex. **Left, from top to bottom:** *reconditus; subrufescens; spatha; osgoodi.* Note the clear-cut black terminal portion and tendency towards a broader, more spatulate shape in all. **Right, top to bottom:** two tails of *aequatorialis*; note the virtual absence of black and the narrow shape of the racquets; two tails of *microstephanus*: note the narrower, duller black posterior portions, racquets broader than those of *aequatorialis* but narrower than those of *subrufescens* and allies.

Analyses of plumage color and pattern

DISCRIMINANT ANALYSIS: (Fig. 9).- The first three

discriminant functions included over 91% of the total variation among taxa in the 14 plumage characters, and the first four, over 96%. Loading most heavily on the first function were characters 14 (-0.536), 6 (-0.417), 8 (0.369) and 5 (0.364); on the second function were character 1 (0.536), 6 (0.535), 10 (0.307) and 8 (0.304); on the third function, character 2 (0.781) and 9 (0.591) and on the fourth, character 13 (0.500), 14 (-0.436), 8 (-0.385) and 6 (-0.383). The first two functions (Fig. 9a) separated *aequatorialis* and *lessonii* completely from the remaining forms, while separating *momota* and *microstephanus* nearly completely from *conexus, reconditus, subrufescens, osgoodi, argenticinctus* and *bahamensis.* The members of this "*subrufescens* group" formed a single cluster with no clear separations. The main effect of the third function (Fig. 9b) was to separate *bahamensis* nearly completely from the remaining members of this cluster; the fourth function mainly separated *momota* (albeit not completely) from *microstephanus*. The overall results of the analysis including all the discriminant functions (Table 3) clearly separated *aequatorialis* and *lessonii*: in each, all specimens were classified correctly and no specimen of any other taxon was classified with either, thus each was 100% diagnosable on the basis of plumage pattern. Forming a nearly distinct cluster were *microstephanus* and *momota* with 98.6% separation from the remaining taxa (only 2 of 145 total specimens misclassified on the basis of plumage). Of the "*subrufescens* group", only *bahamensis* was separated at a statistically significant level (2 of 98 specimens misclassified, 98.0% discrimination). Excluding *bahamensis*, the most distinct of the remaining taxa was *argenticinctus*, 90.4% discriminated from the rest of the group (8 of 83 total specimens misclassified). Leaving aside the preceding two taxa, only *osgoodi* was over 50% diagnosable from the remainder of the "*subrufescens* group" by plumage.

Measurements of external characters

Several features were immediately evident from the external measurements of the ten taxa (Appendix 11): the large size of *aequatorialis*, the small size of all members of the "*subrufescens* group" except *bahamensis,* and the considerable difference in size between *microstephanus* and *momota*. In virtually all measurements and for all taxa, male motmots averaged larger than females although nearly always with considerable overlap. Only a small minority of the t-tests for different measurements indicated significant sexual dimorphism (3 of 50 tests with the Bonferroni correction, 13 of 50 without) and the tests giving significant results were scattered among the different measurements and taxa: no consistent pattern was evident (Table 4). Because of the possibility of missexed specimens in these sexually monochromatic birds (especially since the majority of specimens measured were >50 years old and lacked specific gonad data), I combined the sexes for analysis, which also permitted the inclusion of unsexed birds. One-way ANOVA for total culmen, bill length from nostril, height of bill at nostril, chord of folded wing and tail length all showed highly significant variation among taxon means (Table 5). The most consistent result of all tests was the clear separation of *aequatorialis* from all other taxa due to its large size. At the other extreme were the small taxa *conexus, reconditus, subrufescens, osgoodi* and *argenticinctus,* among which very few significant differences and no clear separations among taxa were found. Second largest in most measurements was *momota,* followed by *bahamensis* (bill dimensions) or *lessonii* (wing) and *microstephanus*. In bill and tail dimensions *lessonii* fell within the "*subrufescens* group"; *bahamensis* was significantly larger than the other members of this group except in tail length: indeed, it was the shortest-tailed of all forms considered here (cf. Table 6 and Appendix 11). These differences in the ordering of the various taxa in ANOVA indicate that, in addition to differences in absolute size, there were differences in shape between taxa.

PCA 1: COMPARISON OF SHAPE PARAMETERS USING RELATIVE MEANS OF EXTERNAL MEASUREMENTS (Table 6, Fig. 10): The first axis accounted for 94.9% of the variation in multivariate space, and the second axis contributed a further 3.8%. The resulting analysis placed *bahamensis* in the extreme upper left of the graph,
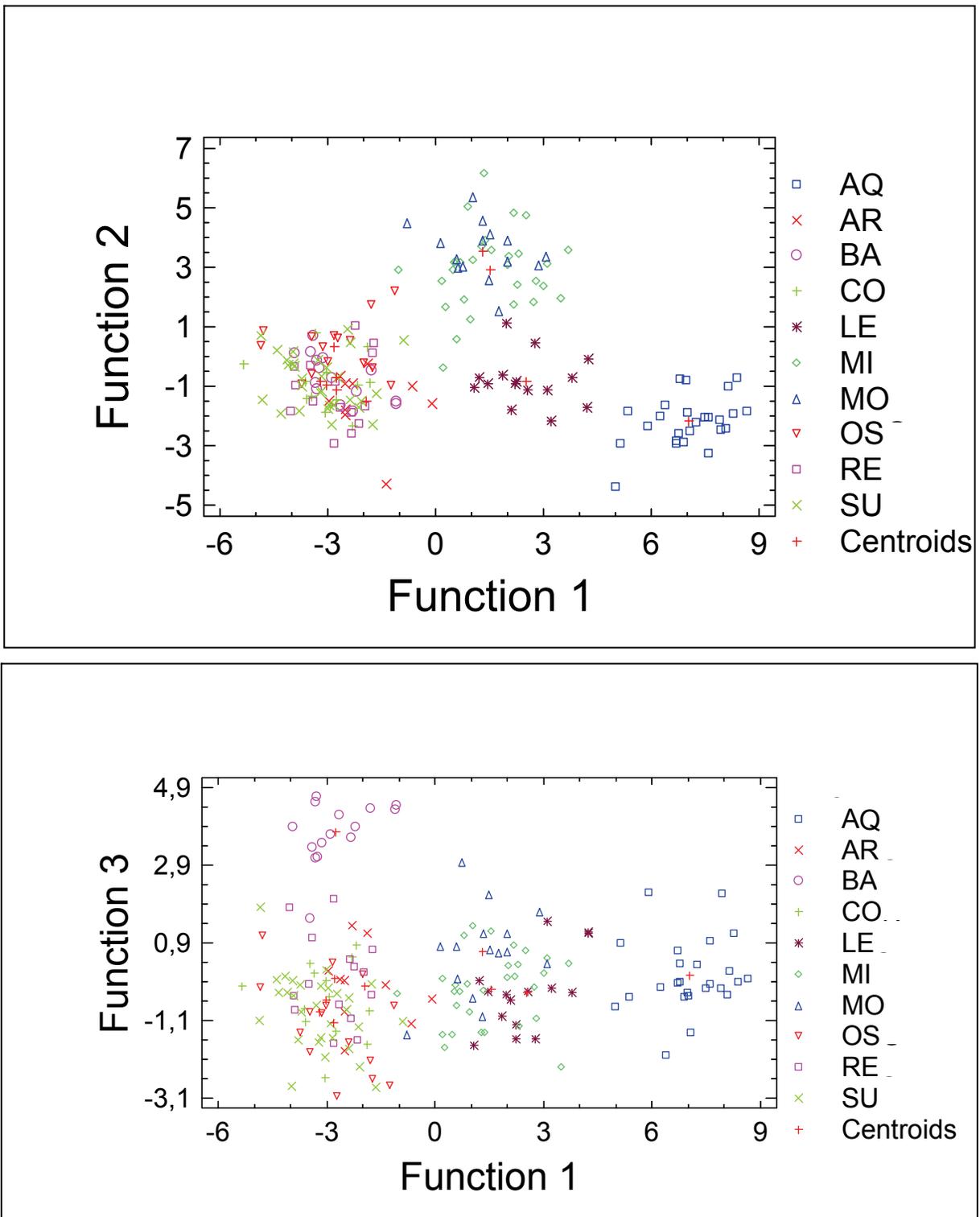
Figure 9. Plot of discriminant analysis of 183 individuals of ten taxa of the "*Momotus momota* complex" based on 14 plumage characters. **a.** Discriminant functions 1 and 2. Note the complete separation of *aequatorialis* and *lessonii* from all other taxa; the nearly complete separation of (*momota + microstephanus*) from the remaining taxa, which form the "*subrufescens* group". **b.** Discriminant functions 1 and 3. The main effect of this function is the nearly complete separation of *bahamensis* from the remaining members of the "*subrufescens* group".

Table 3. Results of discriminant analysis of ten taxa[1] of the *Momotus momota* complex based upon 14 characters of plumage patterns.

		Predicted taxon									
		AQ	LE	MI	MO	CO	RE	SU	OS	AR	BA
Actual taxon	AQ n=25	25 100%	0	0	0	0	0	0	0	0	0
	LE n=15	0	15 100%	0	0	0	0	0	0	0	0
	MI n=30	0	0	23 76.7%	6 20.0%	0	0	0	0	1 3.3%	0
	MO n=15	0	0	1 6.7%	14 93.3%	0	0	0	0	0	0
	CO n=13	0	0	0	0	6 46.2%	2 15.4%	3 23.1%	1 7.7%	1 7.7%	0
	RE n=15	0	0	0	0	2 13.3%	7 46.7%	2 13.3%	1 6.7%	2 13.3%	1 6.7%
	SU n=30	0	0	0	0	6 20.0%	4 13.3%	15 50.0%	2 6.7%	3 10.0%	0
	OS n=15	0	0	1 6.7%	0	2 13.3%	1 6.7%	2 13.3%	9 60.0%	0	0
	AR n=10	0	0	0	0	0	1 10.0%	0	0	9 90%	0
	BA n=15	0	0	0	0	0	0	0	1 6.7%	0	14 93.3%

1 = Abbreviations of taxa: AQ = *aequatorialis*; LE = *lessonii*; MI = *microstephanus*; MO = *momota*; CO = *conexus*; RE = *reconditus*; SU = *subrufescens*; OS = *osgoodi*; AR = *argenticinctus*; BA = *bahamensis.*

Table 4. Sexual dimorphism in ten taxa of the *Momotus momota* complex: values and probabilities of Student's t-tests comparing male and female means for different measurements (see Appendix 11). Sample sizes of males and females in parentheses. Value of t given with its associated p value; with Bonferroni correction, a p of less than 0.008 is required for a significant diference.

Taxa	Measurements				
	Length of total culmen	Bill length from nostril	Height of bill at nostril	Chord of closed wing	Total length of tail
lessonii (25,20)	1.72 (p = 0.093)	1.94 (p = 0.059)	2.35 (p = 0.023)	2.23 (p = 0.031)	1.87 (p = 0.068)
conexus (23,25)	2.38 (p = 0.022)	1.94 (p = 0.059)	1.69 (p = 0.010)	1.53 (p = 0.133)	1.18 (p = 0.243)
reconditus (28,22)	1.65 (p = 0.105)	0.66 (p = 0.510)	0.81 (p = 0.422)	1.36 (p = 0.182)	0.19 (p = 0.849)
subrufescens (35,33)	1.66 (p = 0.101)	2.67 (p = 0.010)	1.16 (p = 0.150)	2.27 (p = 0.026)	1.83 (p = 0.072)
osgoodi (7,8)	0.71 (p = 0.489)	2.60 (p =0.022)	1.01 (p = 0.233)	1.56 (p = 0.142)	0.52 (p = 0.612)
bahamensis (11,5)	0.25 (p = 0.803)	0.450 (p = 0.665)	0.32 (p = 0.753)	2.08 (p = 0.056)	0.210 (p = 0.833)
argenticinctus (12,6)	1.11 (p = 0.281)	1.45 (p = 0.167)	0.71 (p = 0.488)	1.39 (p = 0.182)	0.60 (p = 0.571)
microstephanus (67,51)	1.15 (p = 0.252)	1.71 (p = 0.089)	0.95 (p = 0.343)	5.78 (p < 0.001)	2.69 (p = 0.008)
momota (12,10)	1.63 (p = 0.123)	2.88 (p = 0.009)	4.63 (p < 0.001)	1.67 (p = 0.110)	1.58 (p = 0.130)
aequatorialis (44,34)	2.20 (p = 0.032)	1.75 (p = 0.084)	1.88 (p = 0. 064)	1.00 (p = 0.334)	2.97 (p = 0.005)

with *lessonii* closer to the center; *aequatorialis* was isolated to the upper right, and *microstephanus* and *momota* fell to the lower left. In the center, the remaining members of the "*subrufescens* group" formed a fairly compact cluster, approached by *momota* (Fig. 10). Overall, the analyses of biometrics tended to confirm the four main groups found by analysis of plumage characters; moreover, *bahamensis* was even more clearly separated from the "*subrufescens* group" by virtue of its relatively long wing and short tail and formed a distinct fifth group. The remaining members of the "*subrufescens* group" were remarkably uniform not only in size but also in shape parameters.

PCA 2: COMPARISON OF RELATIVE MEANS OF MORPHOLOGICAL MEASUREMENTS AND MEANS OF PLUMAGE CHARACTERS (Fig. 11, data from Table 6 and Appendices 2-9): Combining plumage and relative measurements in a single correlation-based analysis recovered the same five groups as the preceding analyses: *aequatorialis* and *lessonii* widely separated from each other and all other taxa, *momotus* and *microstephanus* forming a cluster near but separated from the compact cluster formed by members of the "*subrufescens* group" with the first two principal components; and with *bahamensis* widely separated from the rest of the "*subrufescens* group" on the third component (indeed, nearly as widely as *lessonii* or *aequatorialis*). The first three component axes accounted for 49.6, 27.9 and 9.9%, respectively, of the total variation. Factors loading most heavily on PC1 were relative length of total culmen (-0.343) and plumage characters 5 (-0.346), 14 (-0.340), 7 (0.321), 2 (0.0.314) and 1 (-0.304). On PC2, relative wing length (0.435) and plumage characters 10 (0.413), 9 (-0.387), 6 (-0.370) and 11 (-0.359) loaded most heavily while relative tail length (0.667) and plumage characters 8 (-0.350) and 2 (0.328) were most important.

Description and measurements of the "primary song"

Based on the structure of their hooting primary songs, the taxa considered here break into two groups: those with two-note songs, and those with

the usual songs consisting of a single hoot. *Aequatorialis, lessonii, microstephanus* and *momota* comprise the "two-hoot" group; the single-hoot group includes *conexus, reconditus, subrufescens, osgoodi, argenticinctus* and *bahamensis*. However, in two of the four cuts of *bahamensis* available to me, one bird gave a double hoot when countersinging with a second bird (that was giving the usual single hoot). In one instance the recordist (A. Jaramillo) stated that the two birds in question were a pair sitting close to one another. In the 17 recordings of other members of the one-hoot group, only single hoots were given including several apparent instances where two birds were evidently responding to one another. My own limited experience agrees: nearly all countersinging bouts I have heard (of *subrufescens* and *reconditus*) were strictly single-hoot performances. However, I once heard an individual of *subrufescens* give a double hoot in response to playback, although other individuals in the near vicinity were responding with single hoots. If given by other members of the "*subrufescens* group" besides *bahamensis*, double hoots are seemingly infrequent and might be restricted to countersinging in close proximity by pair members - but much more recording effort will be needed to document this.

Among the two-hoot group, the most similar in note structure were *microstephanus* and *momota*; in both, the song sounds like "hoo-dup" with the first note longer and rising in pitch, the second note more abrupt. The sonograms (Fig. 12) showed the first note rising in frequency and falling abruptly at the end; the second note rose and fell very abruptly and was much shorter. The taxa seemed to differ mainly in that the song of *momota* was lower-pitched and slower than that of the smaller *microstephanus,* although a larger sample of songs of *momota* would be needed to confirm this. Although much the largest of the taxa considered here, *aequatorialis* had a surprisingly high-pitched and rapid song, sounding like a fast "hudup". The two notes were both short, of nearly equal lengths and frequencies; the notes rose and fell abruptly producing an inverted "u" on the sonograms with an extremely short interval between them (Fig. 12). The notes of the

Table 5. Results of one-way analyses of variance of means of morphological measurements of all adult individuals (sexes combined, unsexed birds included) of ten taxa of the *Momotus momota* complex from southern Central and northern South America.

| Parameter	F	p	Groups (In order of decreasing size, left to right)
Length of total culmen	60.21	<0.0001	AQ>MO≥BA=LE≥MI≥RE=AR=OS=CO=SU
Length of bill from nostril	44.70	0.0006	AQ>MO=BA≥MI≥CO=RE=LE=AR=OS=SU
Depth of bill at nostril	87.54	<0.0001	AQ>MO=BA≥MI≥CO=RE=LE=OS=AR=SU
Chord of closed wing	390.6	<0.0001	AQ>MO>LE=BA≥MI>RE=AR=OS=SU=CO
Length of tail	259.6	<0.0001	AQ>MO>RE=CO=LE=MI=AR=OS=SU=BA

For abbreviations of taxon names, see Table 3; for sample sizes, see Table 6.

Table 6. Means and standard deviations of measurements (in mm) of ten taxa of the *Momotus momota* complex. Relative means were obtained by dividing the mean linear measurements by the cube root of the mean body mass for each taxon.

Parameter	LE	AQ	CO	RE	SU	OS	BA	AR	MI	MO
Body mass (g)										
n	32	23	4	12	27	5	15	3	21	13
mean	115.48	163.48	93.78	98.13	96.04	95.10	111.40	96.27	120.71	145.08
sd	11.38	14.54	4.91	11.65	12.63	11.40	13.13	8.43	13.98	13.88
cube root	4.8697	5.4679	4.5433	4.6125	4.5795	4.5645	4.8117	4.5831	4.9421	5.2546
Total Culmen										
n	43	78	35	48	90	15	20	18	118	22
mean TC	43.98	48.49	41.76	42.57	41.61	41.89	44.15	42.22	43.42	45.68
sd	2.45	1.93	1.78	2.47	2.32	1.64	2.04	2.95	1.89	2.74
mean rel TC	9.031	8.867	9.192	9.229	9.087	9.177	9.176	9.213	8.786	8.693
Bill from nostril										
n	43	78	35	48	90	15	20	18	112	22
mean BFN	28.96	33.03	29.09	28.99	27.95	28.55	29.51	28.82	29.31	30.57
sd	2.14	1.80	1.77	1.89	1.78	1.12	1.46	2.36	1.57	1.74
mean rel BFN	5.946	6.041	6.402	6.285	6.103	6.256	6.133	6.289	5.930	5.818
Bill height at nostril										
n	44	73	35	47	86	15	20	18	110	21
mean BH	11.61	13.28	11.79	11.76	11.19	11.49	12.14	11.49	11.87	12.50
sd	0.59	0.48	0.51	0.44	0.51	0.64	0.41	0.53	0.48	0.61
mean rel BH	2.383	2.429	2.595	2.550	2.443	2.518	2.522	2.507	2.403	2.380
Length of closed wing										
n	44	79	35	50	91	15	17	18	118	22
mean WL	135.68	155.92	124.35	127.46	124.58	125.29	135.15	126.41	131.78	142.43
sd	3.84	5.12	4.31	2.98	3.79	3.65	2.20	4.14	3.87	3.84
mean rel WL	27.863	28.515	27.371	27.634	27.205	27.448	28.088	27.581	26.665	27.105
Tail length										
n	43	76	34	40	80	14	20	17	100	21
mean TL	227.64	294.18	231.21	232.13	223.13	224.64	221.70	225.41	227.51	258.05
sd	8.63	14.87	10.48	10.08	10.50	11.96	9.67	9.42	10.83	9.94
mean rel TL	46.746	53.801	50.890	50.325	48.724	49.215	46.075	49.183	46.035	49.109
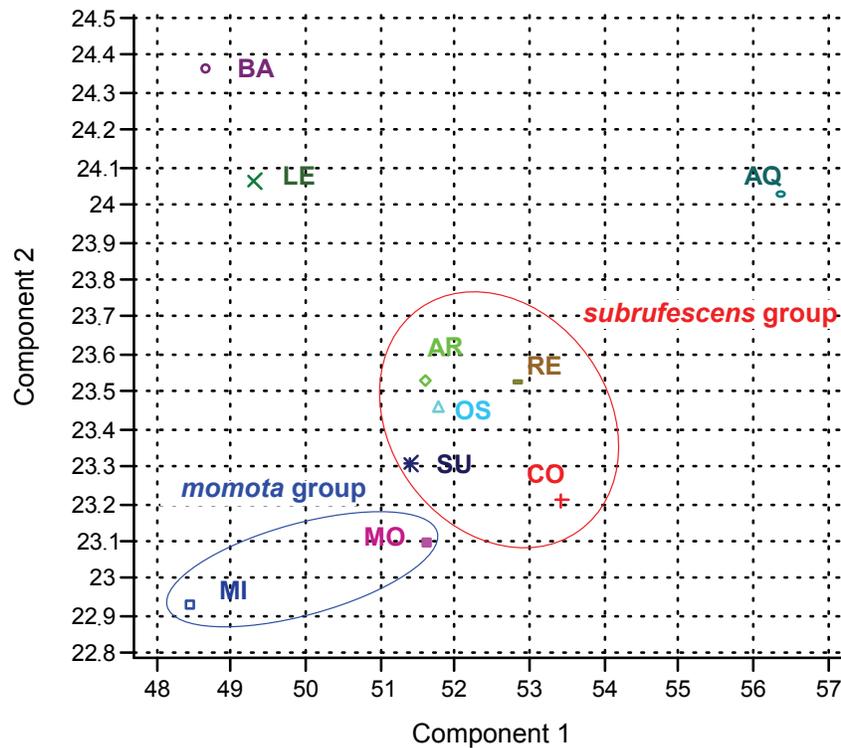
Figure 10. Principal components analysis of the relative means of five morphological measurements among ten taxa of the "*Momotus momota*" complex. Note the compact "*subrufescens* group" at center, the "*momota* group" at lower left, and the widely separated taxa *lessonii*, *aequatorialis* and especially, *bahamensis*.
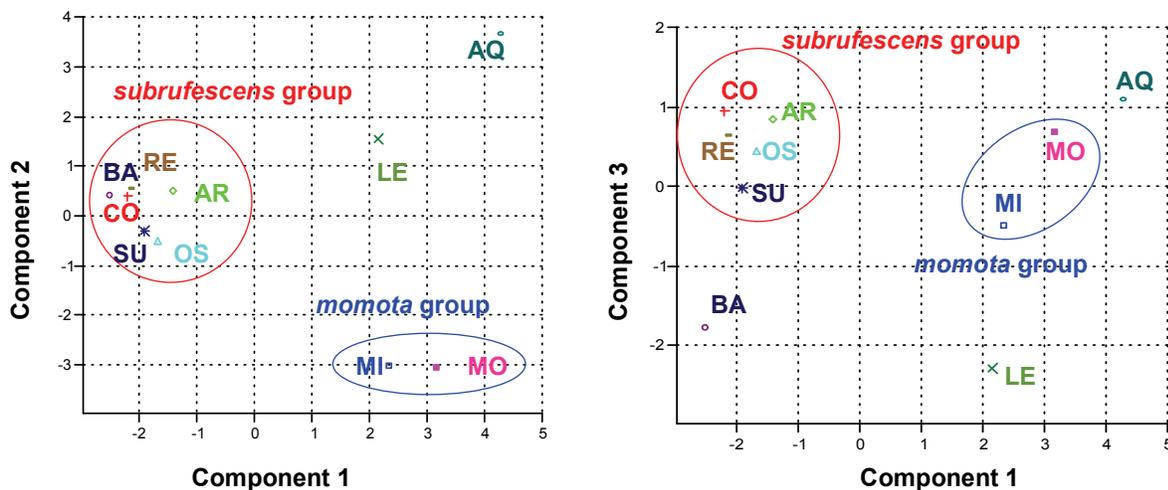
Figure 11. Principal components analysis of the relative means of five morphological characters and 14 characters of plumage pattern for ten taxa of the "*Momotus momota* complex*". Note the compact clustering of the *subrufescens* group on all three components, except that *bahamensis* separtes widely from the rest on component 3; the *momota* group is well defined on all three principal components, and *aequatorialis* and *lessonii* are distinct on all three.

song of *lessonii* were less structured, rising and falling less noticeably; the two notes were quite similar in frequency and structure. However, the main distinguishing feature of the song of *lessonii* was the long interval between notes, much longer than either of the notes themselves (Fig. 12); the song sounds like "hup, hup".

The primary song of the members of the one-hoot group consisted of a single "whooping" note starting low, gradually rising in pitch and intensity, then tailing off briefly at the end (Fig. 13): it sounds like "hooOOp". This note was considerably longer than the initial note in the songs of any of the two-note group. However, there was considerable variation in the duration and frequency of this note among these taxa. The notes of *subrufescens, conexus* and *reconditus* were the most similar, agreeing in length and in being high-pitched (peak frequencies usually near or exceeding 500 Hz); the main difference in the recorded songs was in the initial frequency (Fig. 13). Most distinctive was *osgoodi*, with its lower-pitched, long-drawn-out note. At the other extreme was *argenticinctus*, which had a notably short song that rose and fell relatively less. The single-note song of *bahamensis* was most similar to that of *argenticinctus* in both respects, interesting in that both are isolated taxa at the opposite geographic extremes of the one-note group. However, in songs of *bahamensis* the ending was much more abrupt than in other members of the one-hoot group, in which a clear drop in frequency and amplitude at the end was evident (Fig. 13); more recordings will be required to determine whether this difference is consistent and clear-cut. The first note of the two-note songs of *bahamensis* averaged shorter and lower-pitched than the single-note song, and fell more noticeably in pitch (but less in intensity) at the end. The second note of its two-hoot songs differed from all the corresponding notes of the two-note group in its amorphous structure: its highest frequency and intensity were in the middle but it did not rise or fall in pitch appreciably and there was little indication of the inverted-U trace on the sonograms so evident in the notes of *momota, microstephanus* and *aequatorialis* in particular (Fig. 13, cf. Fig. 12).

**Analysis of features of the "primary song"**

The measured characteristics of the songs of all taxa are given in Table 7. I expressed the frequency variables in Hz and used a correlation-based, rather than variance-covariance analysis because two different kinds of variables were included (frequency and duration). In order to include all taxa in a single analysis, I first compare the characteristics of the single hoots of the one-note group and the initial notes of the two-note group, considering separately the single hoot and initial note of the double hoot of *bahamensis*. The objective of this analysis was to determine whether the first note of the two-hoot group was similar to the single note of the one-hoot group, such that the second note could be considered as simply an addition to a similar single hoot (or alternatively, the one-note group had simply lost the second note of the two-hoot group), or whether the initial note differed in other characteristics. The second analysis treats in more detail both notes of the two-hoot group, including the two-note songs of *bahamensis,* and the third analysis deals exclusively with the one-hoot group.

PCA 3: CHARACTERISTICS OF THE SINGLE HOOT OF THE ONE-NOTE TAXA AND THE INITIAL HOOT OF THE TWO-NOTE TAXA (Table 7, Fig. 14): The first principal components axis accounted for 80.2% of the variation in song parameters among taxa, the second axis for 16.9%; parameters loading most heavily on the first component were those related to note duration and shape (d_1, 0.892; a_1, 0.330); the second component loaded mostly parameters of note frequency (initial frequency -0.593, peak -0.485, terminal -0.549). These two components separated the two-note taxa to the left, the one-note singers to the right of the graph. However, among the former *microstephanus* approached the two-note group rather closely, although apart in the same direction (towards the upper left) as the much more distant *momota*; *aequatorialis* was widely separated towards the lower left, *lessonii* less distant at center left. The shorter notes and lower frequencies separated all these taxa from the one-hoot group. Among the one-note group, *osgoodi* was widely separated at the upper right reflecting its lower-pitched hoot, but the remaining taxa,
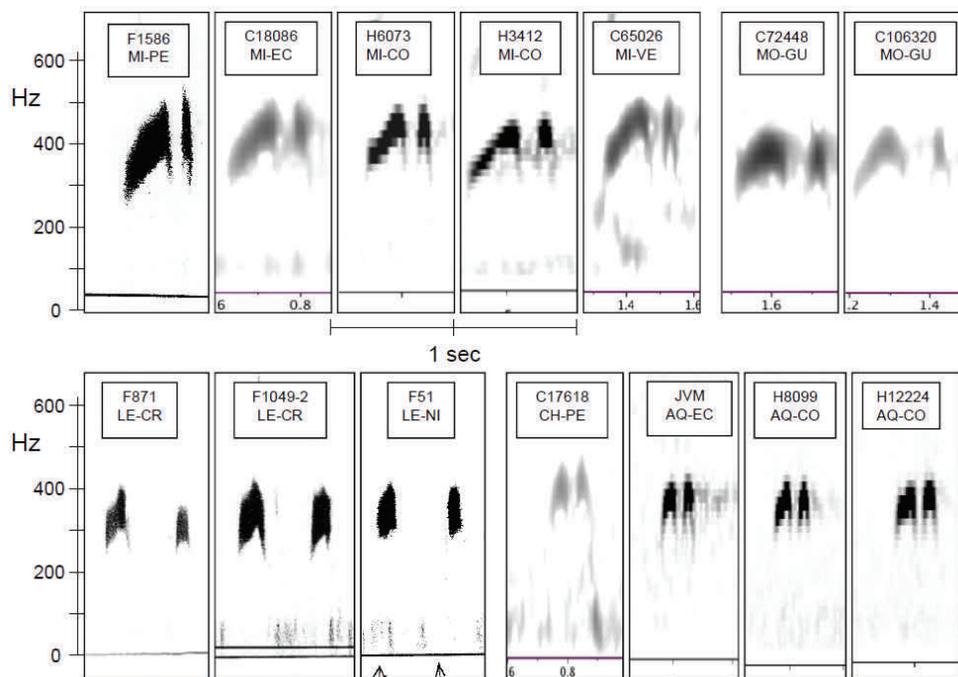
Figure 12. Sonograms of the primary songs or "hoots" of members of the "two-hoot" group of taxa. Upper left: five songs of *M. m. microstephanus* from Peru (1), Ecuador (1), Colombia (2) and Venezuela (1). Upper right: two songs of *M. m. momota* from Guyana. Lower left: two songs of *M. m. lessonii* from Costa Rica and one from Nicaragua. Lower right: one song of *M. m. chlorolaemus* from Peru, and three of *M. m. aequatorialis*, one from Ecuador and two from Colombia. All are to the same scale. For localities, names of sound archives and recordists, see Appendix 1.
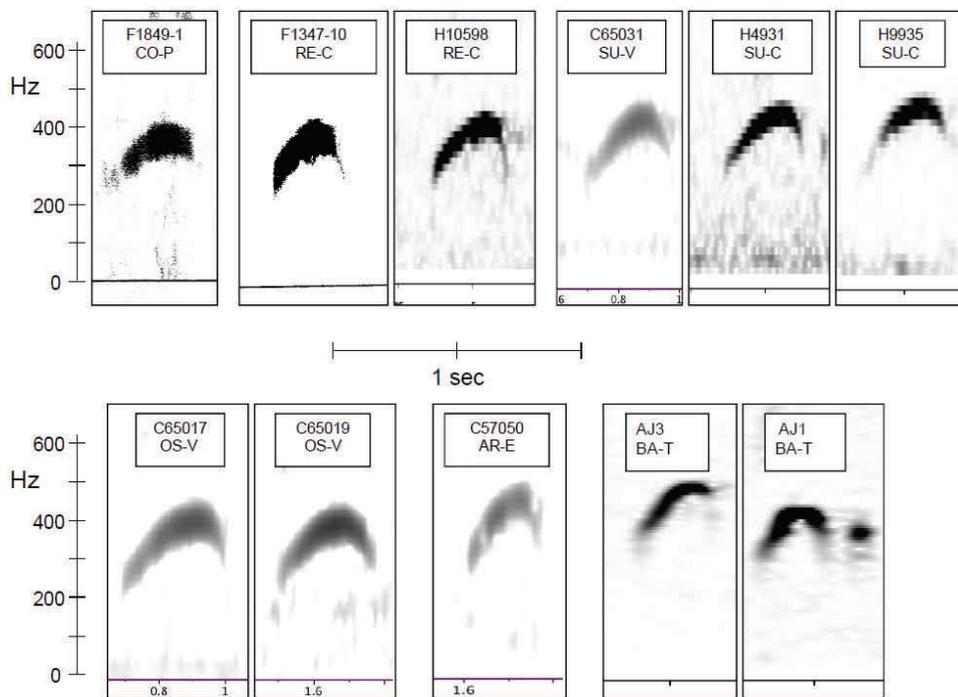
Figure 13. Sonograms of primary songs of several of the "single-hoot" taxa of the "*Momotus momota* complex". Top row, from left: one song of *conexus* from Panamá; two of *reconditus* from Colombia; one of *subrufescens* from Venezuela and two from Colombia. Bottom row: two songs of *osgoodi* from Venezuela; one of *argenticinctus* from Ecuador; and the one-note and two-note (duet) songs of *bahamensis* from Trinidad. For names of sound archives, recordists, localities and collection numbers, see Appendix 1.

Table 7. Means and standard deviations of measurements of songs of members of the *Momotus momota* complex in northern South America and adjacent areas. Time measurements (d) in msec; measurements of frequencies (f) in Hz. For abbreviations see Fig. 3.

| Taxon	Ni	d_1	da_1	d_{1-2}	d_2	da_2	fi_1	fp_1	ft_1	fi_2	fp_2	ft_2
lessonii	5	115.7	82.9	236.3	72.0	55.1	370.1	408.0	384.4	380.7	399.8	387.8
		±12.3	±12.0	±2.1	±12.4	±9.8	±103	±7.5	±15.5	±13.0	±13.3	±16.3
aequatorialis	10	68.7	43.7	33.6	41.7	21.6	388.8	459.9	424.5	424.0	461.9	429.7
		±7.3	±6.8	±4.7	±6.9	±3.0	±26.7	±18.1	±16.3	±29.0	±16.2	±20.5
microstephanus	20	139.7	110.2	40.2	42.2	28.2	303.7	435.2	396.3	392.0	425.7	373.5
		±23.5	±24.0	±7.1	±4.0	±2.1	±23.6	±23.4	±29.8	±33.6	±30.4	±29.4
momota	2	127.2	83.5	50.7	44.3	18.7	284.2	375.7	341.6	341.2	376.7	339.8
		±12.0	±4.2	±17.7	±18.1	±8.8	±2.6	±30.2	±5.7	±4.9	±22.2	±19.1
conexus	2	227.0	141.9	0.0	0.0	0.0	344.6	492.1	459.3			
		±15.6	±6.5				±1.5	±7.7	±10.3			
reconditus	2	241.8	141.0	0.0	0.0	0.0	330.8	499.8	455.7			
		±13.9	±10.4				±14.8	±1.6	±4.7			
subrufescens	6	218.3	140.7	0.0	0.0	0.0	374.0	509.5	469.7			
		±40.0	±36.7				±48.1	±15.9	±31.3			
osgoodi	4	289.7	210.0	0.0	0.0	0.0	287.1	444.0	378.2			
		±14.3	±23.6				±13.7	±8.3	±29.9			
argenticinctus	3	187.0	135.1	0.0	0.0	0.0	341.1	455.9	405.2			
		±13.0	±8.1				±9.4	±31.8	±7.7			
bahamensis (song)	6	181.6	124.3	0.0	0.0	0.0	362.5	479.8	456.2			
		±12.3	±11.3				±28.6	±21.7	±20.3			
bahamensis (duet)	2	167.7	111.7	53.3	61.5	30.8	345.5	453.0	407.8	410.3	416.5	412.7
		±29.2	±17.9	±4.2	±9.2	±4.5	±42.2	±40.5	±46.9	±66.0	±64.3	±63.2

Table 8. Ratios of measurements of various parameters of the songs of members of the *Momotus momota* complex in southern Central and northern South America.

	N	pa_1	pa_2	d_2/d_1	d_{1-2}/d_1	d_{1-2}/d_2	fp_1/fi_1	ft_1/fi_1	fp_2/fi_2	ft_2/fi_2	fp_1/fp_2
lessonii	4	0.715	0.763	0.621	2.067	3.345	1.027	1.038	1.050	1.019	1.021
		±0.035	±0.011	±0.045	±0.218	±0.543	±0.022	±0.024	±0.013	±0.021	±0.028
aequatorialis	10	0.636	0.520	0.612	0.498	0.830	1.871	1.096	1.092	1.015	0.996
		±0.067	±0.034	±0.102	±0.107	±0.202	±0.066	±0.052	±0.041	±0.034	±0.023
microstephanus	20	0.789	0.433	0.302	0.288	0.951	1.433	1.305	1.087	0.954	1.023
		±0.078	±0.040	±0.064	±0.061	±0.200	±0.087	±0.092	±0.040	±0.032	±0.038
momota	2	0.656	0.420	0.349	0.399	1.155	1.344	1.202	1.056	0.986	0.997
		±0.283	±0.176	±0.143	±0.133	±0.217	±0.088	±0.011	±0.052	±0.028	±0.021
conexus	2	0.625	-	-	-	-	1.429	1.333	-	-	-
		±0.015					±0.028	±0.035			
reconditus	2	0.583	-	-	-	-	1.516	1.382	-	-	-
		±0.009					±0.071	±0.047			
subrufescens	6	0.635	-	-	-	-	1.379	1.266	-	-	-
		±0.123					±0.142	±0.096			
osgoodi	4	0.724	-	-	-	-	1.549	1.318	-	-	-
		±0.060					±0.048	±0.086			
argenticinctus	3	0,72404	-	-	-	-	1.336	1.189	-	-	-
		±0.040					±0,066	±0,040			
bahamensis (song)	6	0.684	-	-	-	-	1.327	1.256	-	-	-
		±0.025					±0,060	±0,057			
bahamensis (duet)	2	0.667	0.502	0.368	0.326	0.882	1.311	1.184	1.016	1.006	1.093
		±0.009	±0.002	±0.009	±0.082	±0.201	±0.043	±0.008	±0.006	±0.008	±0.072
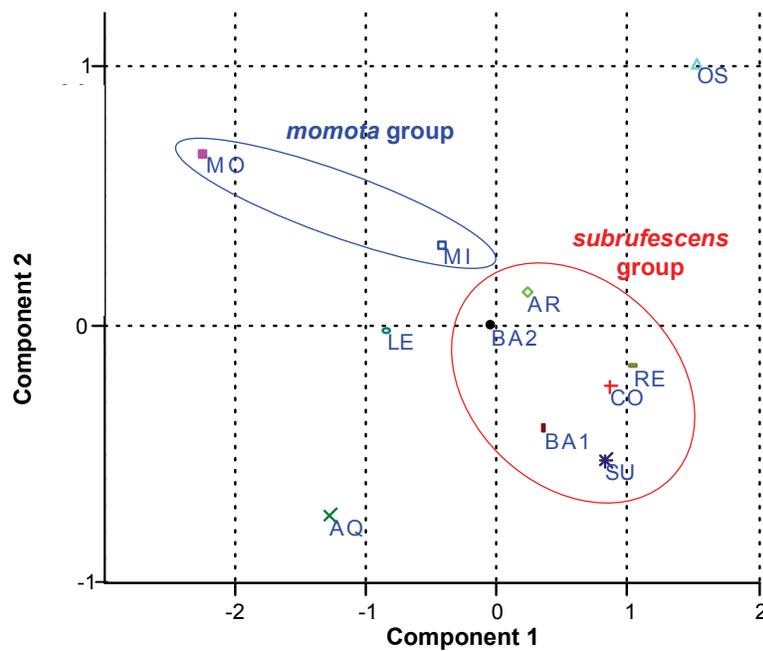
Figure 14. Principal component analysis of five parameters of the primary songs of ten taxa of the *Momotus momota* complex. Abbreviations of taxa as in Fig. 1. The single hoots of the one-note taxa are analyzed with the first hoot of the two-note taxa to determine whether these notes are similar: in effect, whether the presence or absence of a second note represents a simple addition or deletion. The two-note taxa to the left of the plot are separated from the one-note taxa to the right, of which *osgoodi* (upper right) is the only outlier; the first note of the two-note duet song of *bahamensis* groups with the single hoot of the remaining one-note group rather than with any of the two-note group.
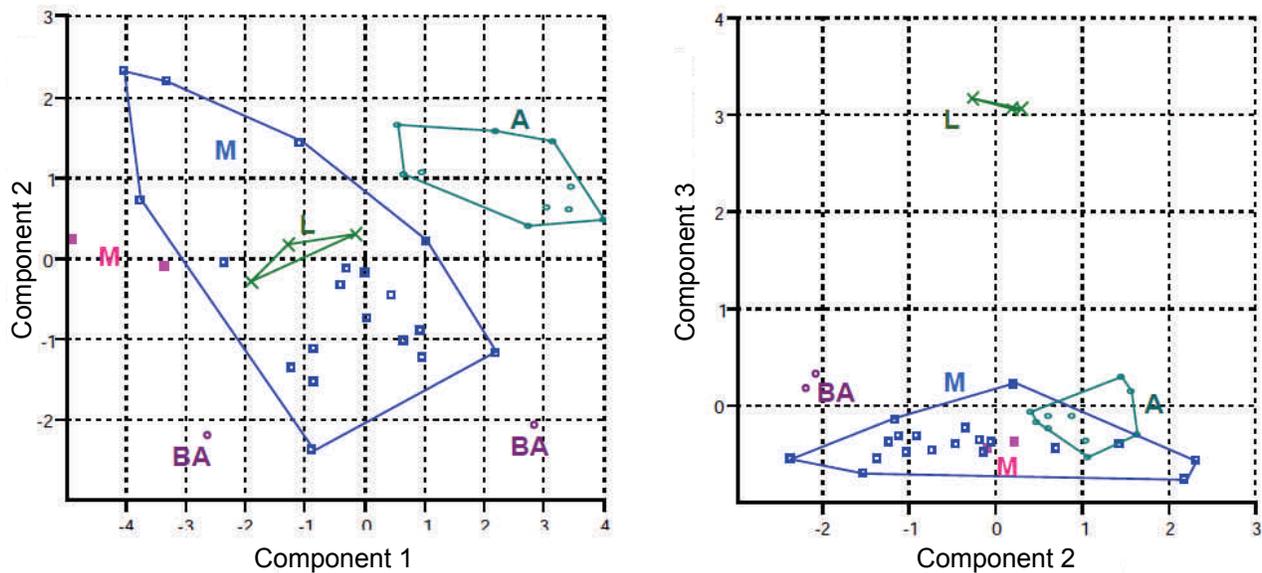
Figure 15. Principal component analysis of 11 parameters of the two-note songs of members of   the *Momotus momota* complex. Included are the primary songs of *aequatorialis* (A), *lessonii* (L), *microstephanus* (M, blue) and *momota* (M, magenta) as well as the two-note duet song of *bahamensis* (BA). Note that *aequatorialis* is segregated from other taxa by components 1 and 2 but not 3, *momotus* from *microstephanus* by 1 but not 2 or 3; *lessonii* separates completely from other taxa on component 3, in which internote interval loads heavily; the two cuts of *bahamensis* spread widely on component 1 but are very close on 2 and 3 and in no case overlap with those of the "true" two-note taxa.
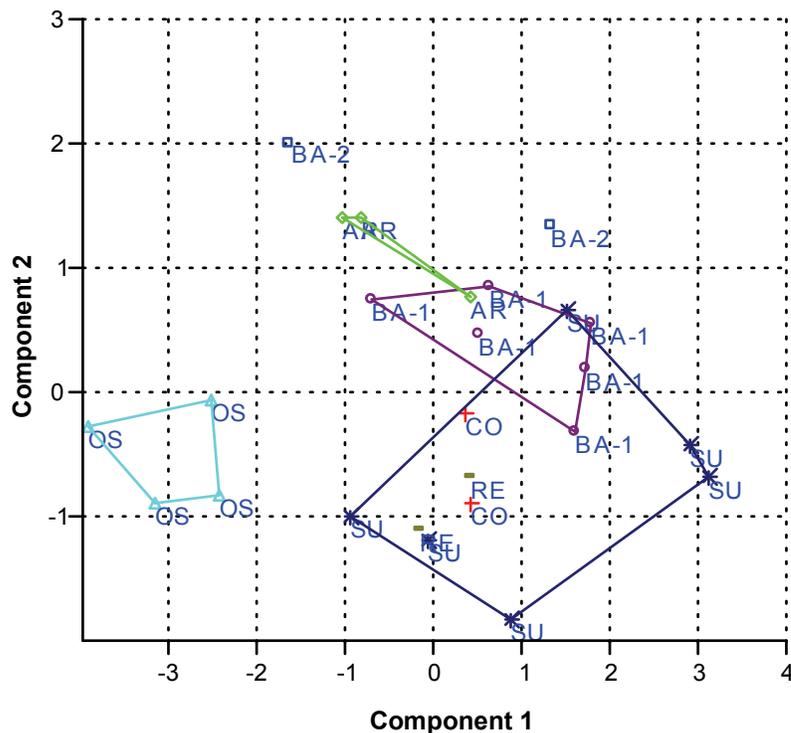
Figure 16. Principal component analysis of six characters of the single hoot of the one-note taxa of the *Momotus momota* complex. Abbreviations of taxa as in Fig. 1. BA-1 indicates the single hoot of the usual song of *bahamensis*; BA-2 indicates the first note of the song given by one member of presumed countersinging pairs. Note that the hoots of *reconditus* and *conexus* are indistinguishable from those of *subrufescens*; those of *argenticinctus* and *osgoodi* are entirely distinct, while the single hoot of *bahamensis* is intermediate between those of *argenticinctus* and *subrufescens* while the first note of its double hoot is distinct.

including both notes of *bahamensis*, formed a fairly compact cluster at the right center of the plot. This tends to reinforce the affinities of *bahamensis* to the "*subrufescens* group", and also indicates that the form and frequency of the single notes of the one-hoot group differ from the first note of the two-hoot group; these differences do not reflect simply the addition or deletion of a second note.

PCA 4: CHARACTERISTICS OF BOTH HOOTS OF THE TWO-NOTE TAXA (Tables 7 and 8, Fig. 15): The results of this analysis are rather less illuminating than those of the preceding one, and tend to emphasize the differences between taxa rather than their affinities. The first axis explained 58.1% of the variation, the second 29.9% and the third, 8.9%. Loading most heavily on the first axis were the duration of note 1 (-0.456) and of the internote interval (-0.250) and the ratio between them (-0.582), and the shape parameters of note 1: pr_1, fp_1/fi_1 and ft_1/fi_1 (-0.379, 0.312 and 0.234). The second axis is most heavily influenced by the durations of note 1 (-0.737), the rising portion of this note (-0.289) and the internote interval

(-0.280) with a lesser contribution from the rising portion of note 2 (-0.223). The graph of these two axes isolates *lessonii* in the lower left-hand corner and *aequatorialis* at the top center; *momota, microstephanus* and *bahamensis* form a cluster to the right, probably reflecting the fact that their initial notes are relatively long and rising. The variables loading most strongly on the third axis are the rising portion of note 1 (-0.782), the duration of note 1 (0.383), and various frequency ratios of this note (0.21-0.25). The main effect of this axis is to separate *bahamensis* from *momota* and, especially, *microstephanus*; plots of this axis with the first or second axes spread the five taxa all over the graph, giving little indication of affinities.

PCA 5: CHARACTERISTICS OF THE SINGLE HOOTS OF THE ONE-NOTE TAXA (Tables 7 and 8, Fig. 16): In this analysis, the first component includes 72.0% of the variation in song features, the second 21.9%. Loading most heavily on the first component are note length (-0.704) and peak frequency (-0.548); on the second, initial frequency (-0.818) and terminal frequency (0.469). On the plot, the most notable result is the complete

separation of *osgoodi* from the remaining taxa to the lower left reflecting mainly its longer and slightly lower-pitched hoot; in the center is the polygon of *subrufescens*, which includes the hoots of *reconditus* and *conexus*. Completely separated from the latter are the hoots of *argenticinctus* towards the upper center, but the single hoots of *bahamensis* overlap both those of *argenticinctus* and *subrufescens*; the two first notes of the double hoot of *bahamensis* are distinct towards the top of the plot, although also separated from each other on the first component.

In sum, the overall conclusion from the vocal analysis effectively mirrors the conclusions from plumage patterns and external morphology: *aequatorialis* and *lessonii* are not close to each other or any other focal taxon; *microstephanus* and *momota* form a group apart, but are more different from each other than are several members of the "*subrufescens* group", which always form a compact cluster (*conexus, reconditus, subrufescens*). The most distinctive of the one-hoot group on the basis of its primary song is *osgoodi*, reflecting its comparatively long-drawn-out, slowly rising hoot; that of *argenticinctus* differs from those of *conexus, reconditus* and *subrufescens* in being somewhat shorter, with less variation in frequency. The single hoot of *bahamensis* is rather intermediate between those of the preceding three taxa and that of *argenticinctus* but ends more abruptly, whereas the first note of its two-hoot song is shorter and slightly lower with less variation in frequency.

DISCUSSION

BIOGEOGRAPHY OF THE "*MOMOTUS MOMOTA* COMPLEX".- Chapman (1923) was the first to attempt to explain the evolution of the Momotidae in general and the "*Momotus momota* complex" in particular, based on present distributions and overall plumage coloration. He considered that the motmots had originally evolved in northern Middle America because they are most diverse there in genera and species (see also Mayr 1964, Howell 1969). He considered southern Mexico and Guatemala to be the center of origin of the genus *Momotus* because only there occur members of

both of his "species-groups", the rufous-crowned (*mexicanus*) and the blue-crowned (*momota, sensu lato*); also, this is the closest continental area to the Greater Antilles, home of the Todidae, the putative closest relatives of the motmots according to Murie (1872), although Hackett et al. (2008) found that the todies are the sister group to a clade formed by motmots and kingfishers.

Noting that *M. lessonii* occurs at progressively higher elevations from southern Mexico to W Panama, Chapman proposed that the initial invasion of South America was by a "*lessonii* stock" that crossed via a "now-subsided Panama subtropical bridge" directly into the subtropical zone of the Andes and spreading thence south, mainly on the E slope, to extreme SE Peru, giving rise to *aequatorialis*. He proposed a separate origin from "pre-*lessonii* stock" of the *momota-subrufescens* groups on his "Panama subtropical bridge"; this group spread through the lowlands of N South America, reaching Trinidad and Tobago before rising sea levels isolated them as land-bridge islands. The split between the *subrufescens* and *momota* groups occurred when a *conexus*-like form crossed the Andes near the headwaters of the Río Magdalena and evolved into *microstephanus*, which spreading east and south through the Guianan and Amazonian lowlands gave rise to the variety of taxa of his *momota* group that now inhabit this wide area. Finally, he postulated that birds from this latter group re-crossed the Andes to the Pacific slope, probably in extreme S Ecuador or N Peru, giving rise to the isolated *argenticinctus*. He based this conclusion largely on the similarity in overall plumage coloration between *argenticinctus* and some races of the *momota* group south of the Amazon, especially *pilcomajensis* of SE Bolivia, S Brazil and Paraguay.

Chapman's hypothesis would explain the greater degree of resemblance between *lessonii* and *aequatorialis* as well as the high degree of divergence of the latter from other South American forms, but the biogeographic scheme contains many untested assumptions (and speculations). His major taxonomic conclusions are in agreement with mine, with one major exception: the affinities

of *argenticinctus*. Hence, there has been need for a modern phylogeographic study employing molecular techniques and to derive a phylogeny and estimate dates of important divergence events. Such a study has been performed by Witt (2004), who has kindly permitted me to quote some of his major conclusions regarding the "*M. momota* complex" here, in advance of a full publication of his work.

Witt (2004) confirmed the northern ("tropical North American") origin of the motmots, which were restricted to Middle America prior to the formation of the Panama isthmus ca. 3.2 million years ago (mya). Before this time, they had divided into two main clades by the end of the Miocene, one including the genera *Hylomanes, Electron* and *Eumomota*, the other comprising *Aspatha, Baryphthengus* and *Momotus*. In the latter clade, *Aspatha* separated from *Baryphthengus* and *Momotus* by the early Pliocene and the latter two had split by the mid-Pliocene. The first movement into South America came with the formation of the land connection via Panama, about when *aequatorialis* diverged from the rest; next came the split between *lessonii* and *subrufescens-momota*, approximately during the early to mid-Pleistocene; this was probably when the proto-*subrufescens/momota* stock reached the South American lowlands. In the meantime, the Andes had reached their greatest elevations at the end of the Pliocene and formed an impassible barrier to gene flow for lowland birds across the main or Central Andes from N Colombia south to at least N Peru from about that time onwards. The divergence of the *subrufescens* and *momota* daughter clades occurred during the mid-Pleistocene, probably when the ancestors of the latter reached the eastern side of the Andes (perhaps, as Chapman suggested, via the head of the Magdalena valley, effectively bypassing the highest elevations).

In Witt's analysis, *argenticinctus* was nested within the *subrufescens* clade, and may have diverged somewhat earlier from the *subrufescens* group than did *bahamensis,* probably indicating an earlier movement of this group down the Pacific coastal plain (although its subsequent isolation due to very wet conditions developing in the southern Chocó region could have occurred rather later, following the last glacial maximum). The splitting off of *bahamensis* occurred relatively recently; at the geographic terminus of the Andes, it is however possible that the Trinidad-Tobago population had begun to differentiate well before rising sea levels severed the land connection to Venezuela's Paria Peninsula. In any case, this population has diverged phenotypically to a much more marked degree than has *argenticinctus*, doubtless reflecting its small size and total isolation during at least the last 10-15,000 years, which could have facilitated fixation of unique alleles via selection or genetic drift. Witt's study thus complements Chapman´s analysis and corrects it at several points, in particular regarding the affinities of *argenticinctus*, where his conclusion is wholly in accord with mine.

SPECIES LIMITS IN THE "*MOMOTUS MOMOTA* COMPLEX".- I now return to my original question: how many species of *Momotus* should be recognized in the area between Nicaragua, Trinidad and N Peru? Analyses of color pattern, external morphology and primary "song" agree in identifying four well-defined, wholly diagnosable groups: *aequatorialis* (with *chlorolaemus*); *lessonii*; *momota* (with *microstephanus*) and the "*subrufescens* group" (including *conexus, reconditus, subrufescens, osgoodi, argenticinctus* and *bahamensis*). In plumage and biometrics, *bahamensis* differs strongly from the other members of this latter group and although I did not attempt to measure color *per se*, its deeper rufous coloration below is also distinctive; it may be separated as a fifth group, although it is less distinct vocally from the remainder of the "*subrufescens* group". The more difficult question is, how many of these groups should be classified as species?

There are a number of recent attempts to define what a species should be, but the notion that species are separately evolving lineages is common to all (de Queiroz 2005, 2007). De Queiroz views the particular criteria advanced by different definitions (diagnosability, reproductive isolation, monophyly, ecological distinctness, etc.) as

secondary properties, none of which is necessary to delimit species. For birds, Helbig et al. (2002) suggest that in practice, two basic properties define species: diagnosability (that is, our ability to distinguish a given group of populations from all others) and lineage integrity (the capacity of a given lineage to maintain its distinctness from other such lineages). An essential corollary of the second element is the probability that the given lineage will maintain its distinctness into the future, including through possible secondary contact with other closely related lineages (cf. Helbig et al. 2002). This requires evaluating the (diagnosable) differences between the lineages in terms of their observed or potential effects on reproductive isolation, the critical point for the "biological species concept" (or definition) as proposed by Mayr (1963) and generalized by Johnson et al. (1999). Although this definition does not mention diagnosability specifically, it clearly assumes it (otherwise we would have nothing to recognize). The related "recognition species concept" (definition) of Paterson (1985) merely restates the biological definition in terms of specific mate recognition mechanisms, probably the most general form of prezygotic reproductive isolating mechanisms. These definitions may be applied directly when populations of two lineages are in contact but their application to differentiated but allopatric populations becomes problematic: the question then becomes, how likely would the observed differences result in reproductive isolation? This is a much more difficult question to answer in many cases, requiring knowledge of the biology not only of the populations concerned but also of related species, and usually requires making inevitably subjective judgments based upon this knowledge. Clearly, this is the case in the "*Momotus momota* complex": each of the four or five diagnosable groups defined above is geographically isolated from all of the others (Fig. 1).

The so-called "phylogenetic species concept" (or definition) of Cracraft (1983) and others, attempts to obviate such potential subjectivity by defining a species as a diagnosable lineage but does not address the question of maintenance of lineage integrity: any absolute difference, however trivial,

would serve to diagnose a species regardless of whether this difference might influence reproductive isolation under sympatry. If one considers maintenance of lineage integrity important, this definition fails because all such differences are not equivalent with respect to reproductive isolation. Its application has resulted in inflating the number of recognized species, including considering as species many allopatric taxa (often named subspecies) that differ in ways most unlikely to influence reproductive isolation. For instance, applying this definition to the taxa treated here would mandate separation of *spatha, argenticinctus* and perhaps *osgoodi* as separate species as well, which I consider to be biologically unrealistic (see below).

Different authors have proposed guidelines for treating differentiated but allopatric populations. Johnson et al. (1999) suggest comparing the differences between the allopatric populations with those between known congeneric, sympatric (and reproductively isolated) species and between intergrading subspecies (cf. also Mayr and Ashlock 1991, Remsen 2005). If the observed differences are of comparable magnitude to those between species, they might function in reproductive isolation were the allopatric populations to enter into contact. The only case of sympatry in the genus *Momotus* is between *lessonii* and the very different (in voice and plumage) *M. mexicanus* in SW Mexico and adjacent Guatemala. Even here, sympatry may be marginal at best as there is apparently some ecological segregation with *mexicanus* in drier or lower habitats, *lessonii* in more humid or upland habitats (cf. Howell & Webb 1994, Howell in litt.). The differences in plumages among the groups of the "*Momotus momota* complex" are less marked than those between any member of this complex and *mexicanus*, in that all of the former have blue diadems or crowns (*mexicanus*, rufous with no blue). This in itself is noteworthy, because the split between *aequatorialis* and all other taxa of *Momotus* apparently occurred before that between *mexicanus* and the remaining members of the complex (see Witt 2004 and below), such that the rufous crown of *mexicanus* may be best considered an autapomorphy. This suggests that the

differences between *aequatorialis* and the remaining members of the complex may be as pertinent as those between the latter and *mexicanus* in judging potential reproductive isolation.

Aequatorialis differs from all other members of the complex in size and proportions, in several aspects of its plumage pattern, in its primary song and in its ecology, being basically a highland bird whereas all other South American taxa are lowland species. In size, proportions, pattern and song the "*subrufescens* group" differs more strongly from *aequatorialis* than do the members of the "*momota* group"; members of this group also occur in drier lowland areas overall. However, a member of the latter group (*microstephanus*) approaches *aequatorialis* closely in distribution (a difference of only ca. 200 m in elevation on the eastern slope of Colombia's Eastern Andes, cf. Hilty & Brown 1986, Salaman et al. 2002) such that local contact (parapatry) between these two is certainly possible, but no indication of hybridization is detectable in the large sample of specimens I examined. Moreover, these two taxa replace one another altitudinally over 2000 km along the eastern face of the Andes (having been recorded to within 250 m of elevation in Peru, cf. Schulenberg et al. 2007) with no hybrids ever reported. I therefore have no hesitation in considering each of these three groups to merit specific recognition. Similarly, *lessonii* is at least as different in plumage from *aequatorialis* as is *momota*, and its primary song is more distinct; it also should be accorded species status.

The case of *bahamensis* is more difficult, as it is clearly an outlying member of the "*subrufescens* group". The differences between *bahamensis* and the other members of the group are clearly much greater than those between the intergrading taxa *conexus, reconditus* and *subrufescens*, but at least vocally, they are less than those between the three two-note groups. Here, the guidelines proposed by Helbig et al. (2002) may prove useful (see also Isler et al. 1999). They recommended specific recognition when: a) all members of at least one age-sex class of one population can be distinguished from all members of the same age-sex class in other populations by at least one qualitative difference; b) all members of at least

one age-sex class can be distinguished from members of the same age-sex class of other populations by nonoverlap in at least one continuously varying character; c) if there is overlap, the members of the same age-sex classes can be completely distinguished by multivariate methods; or d) if most or all members of an age-sex class can be distinguished from that age-sex class of all other populations by two functionally independent characters.

With respect to plumage pattern, *bahamensis* adults are 98% distinguishable from all of the rest of the *subrufescens* group – and if color of the underparts were to be included, they would be 100% distinguishable (Fig. 5). Regarding biometrics, only ca. 4% of all 200+ individuals of *subrufescens, conexus, reconditus, osgoodi* and *argenticinctus* exceed (barely) the minimum values for *bahamensis* in chord of the folded wing, a highly significant statistical difference ($p < 0.001$). There is also a clear difference in proportions (although I was obliged to include only mean values in this PCA, since the data for body masses were independent of those for linear measurements). This is especially noteworthy because the other taxa in this group are remarkably uniform in size and proportions. The differences between *bahamensis* and *subrufescens-reconditus-conexus-osgoodi-argenticinctus* occur in two functionally independent character suites, plumage pattern-color and biometrics. Thus, in two or three of the four criteria of Helbig et al. (2002), *bahamensis* can be accorded (allo)species status. The other taxon of this group nominated for species status, *argenticinctus* (Ridgely & Greenfield 2001), is much less distinct in plumage and indistinguishable from the rest in biometrics, thus I have no hesitation in considering it a subspecies of this group rather than a separate species. Vocally, the differences of *bahamensis* from the others are relatively subtle, but given my small samples of it and *argenticinctus* in particular, more data are required to evaluate the significance of the differences. In any case, the geographic isolation of *bahamensis* is more complete than is that of any other form including *argenticinctus*, which may be (re?) expanding northwards with cutting of the wet forest of NW Ecuador (R. Ridgely in litt.). Since

overwater dispersion seems unlikely in motmots, continued differentiation of *bahamensis* in the foreseeable future seems assured (especially in view of the rising sea levels predicted with global warming): effectively it is on a separate evolutionary trajectory, as required for the "evolutionary species concept" of Wiley (1978). I also note that the specific distinctness of *aequatorialis, lessonii, momota* and *subrufescens* is amply supported by the criteria of Helbig et al. (2002): especially notable are the clear differences in their primary songs.

Each of the four major groups (*aequatorialis, lessonii, momota* and *subrufescens*) form monophyletic clusters in the genetic analysis of Witt (2004), but *bahamensis* is nested within the *subrufescens* group. Therefore, splitting of *bahamensis* would render *subrufescens* paraphyletic. I do not regard this to be a problem because such situations are relatively frequent in birds, where peripatric speciation is common (Funk & Omland 2003). Phenotypic differentiation has clearly proceeded more rapidly in *bahamensis* than in any other member of this group. Effectively, *bahamensis* occupies the isolated low northeastern terminus of the entire Andean chain, whereas *subrufescens* occurs eastward on the coastal slope only to the Caracas region (Hilty 2002).

The recognition of five species in the *"Momotus momota* complex" in the study region essentially represents a return to the classification of Chapman (1923), except that I consider *argenticinctus* to be an isolated member of the *subrufescens* group and not of the *momota* group as did Chapman. By all of the characters analyzed in this study, *argenticinctus* falls unequivocally with *subrufescens* and relatives and not with *momota-microstephanus*. Chapman apparently placed *argenticinctus* with his *momota* because of its similarity in general color pattern to some of the more southern and eastern members of this group, especially *pilcomajensis* (which occurs at closest some 1000 km to the south and east, across the Andes, and is also notably smaller than *microstephanus*). In terms of linear distance, *argenticinctus* is indeed closer to *microstephanus* than to any member of the *subrufescens* group, but

the Andes surely have provided a much more formidable barrier to gene interchange than the currently very wet conditions along ca. 700 km of the Pacific coastal lowlands of Colombia and NW Ecuador that now separate this form from *reconditus*. It is likely that conditions of this region were less humid during glacial periods of the Pleistocene, facilitating the southward movement of the ancestors of *argenticinctus*; also, the lowlands were probably more extensive during glacial periods due to the lowered sea levels. The probable presence of *aequatorialis* in the Andes may also have provided a further impediment to the crossing by a member of the *momota* group.

The original lumping of all of Chapman's species into *M. momota* by Peters (1945), while unjustified by any specific reasons, probably was not entirely arbitrary, as some have suggested. He was simply carrying the "biogeographic species concept" of Hellmayr to its logical conclusion, abetted by the allopatric distributions of all of Chapman's species. His lack of explanation of his actions in specific cases, such as *Momotus*, clearly contributed to the impression of arbitrariness. However, we now have far more information on such topics as distribution, ecology and vocalizations than was available to Peters, as well as far more sophisticated methods of analysis; it is on these bases that many of Peters's lumpings have been shown to be untenable. My analyses indicate that the "*Momotus momota* complex" is another such case.

GEOGRAPHIC VARIATION WITHIN SPECIES, AND STATUS OF SEVERAL NAMED SUBSPECIES.- Within the area of this revision, *lessonii* and *aequatorialis* are monotypic. Other taxa related to *lessonii* occur in Mexico and will not be treated here, but from the descriptions by Ridgway (1911) seem unlikely to deserve species status with the probable exception of *coeruleiceps* with its distinctive all-blue crown. This difference appears to be on the order of that between *bahamensis* and the rest of the *subrufescens* group, although it is worth noting that in this northernmost taxon of the complex, the crown feathers have rather extensive blackish bases, such that the blue in this area is often less solid than around the periphery (somewhat like

some juveniles of several other forms in the complex). However, ongoing studies by Mexican ornithologists appear to support species status for *coeruleiceps* (A. Navarro in litt.). As regards *aequatorialis*, there is no reason to doubt the conspecificity of *chlorolaemus*; the only question is whether the latter is sufficiently different from *aequatorialis* to be recognized at all. I did not examine this point in detail as my sample of *chlorolaemus* was quite small; I will tentatively continue to recognize it pending a more detailed analysis.

Geographic variation in *M. momota* (*sensu stricto*) remains extensive even when *lessonii, subrufescens, aequatorialis* and *bahamensis* are split off from it. The major difference between *momota* and *microstephanus* is size, with *momota* significantly larger; the only difference in color or pattern is the much more extensive (on average) rufous area on the nape of *momota*. However, some *microstephanus* show equally extensive rufous in this area, including specimens far from the range of *momota* and hence not representing (recent) introgression. Meyer de Schauensee (1948-52) ascribed *momota* to Colombia on the basis of specimen(s?) from the western side of the Río Orinoco in Vichada. However, several specimens from this area that I have measured fall within the size range of *microstephanus*, and although one or two have extensive rufous on the nape as do most *momota*, this in itself does not indicate interbreeding and I remain uncertain regarding the presence of *momota* in Colombia. Beyond Colombia and Venezuela, variation in *M. momota* is quite complex: some forms are quite green below, others quite rufescent; particularly southwards, some are also notably smaller than *microstephanus*. Taking the species as a whole, there seems to be a progression in size from the large *momota* in the northeast through the medium-sized *microstephanus* of Colombia and Ecuador, to the small *pilcomajensis* of SW Brazil and E Bolivia. This form is essentially the size of *subrufescens* and has the belly more rusty to ochraceous than the breast – it could be mistaken for a member of the latter group except for the pattern of the diadem, mask and racquets, which ally it with *momota*. The rusty belly of this form

has clearly evolved independently from that of the far distant *subrufescens* group. A thorough study of geographic variation in *M. momota* over all of South America using vocal, chromatic and metric characters is definitely needed, although on present evidence I doubt that more species-level taxa will be recognized.

There is also considerable geographic variation in the *subrufescens* group, which I will consider in more detail as the present study effectively covers the entire distribution of this group. The situation in N Colombia and E Panamá presents an interesting picture, with coloration intensifying from C Panama (*conexus*) to E Darién and extreme NW Colombia (*reconditus*), then becoming paler again westward across N Colombia and into NW Venezuela (*subrufescens*). Birds from the upper Magdalena valley are somewhat darker on average than those from the coastal plain, as a group resembling more closely those from C Panamá, although one individual from the lower middle Magdalena valley is as dark as most *reconditus*. In its strongly rufescent coloration this bird in fact shows a definite approach towards *osgoodi*, which occurs on the opposite side of the low mountains separating the Magdalena and Lake Maracaibo drainages; there may be limited gene flow between these populations across these uplands.

Wetmore (1968) lumped *reconditus* into *conexus* because of lack of diagnosability: he asserted that the range of variation in coloration within each taxon far outweighed the differences between them. I agree, but consider that he did not go far enough – I can see no reason for maintaining *conexus-reconditus* separate from *subrufescens* itself. Over the entire range of these taxa, the intensity of color, especially on the underparts, simply varies with rainfall according to Gloger's rule: darker and more intense in wetter areas like E Darién and N Chocó, paler in drier areas like C Panamá, the Magdalena valley and especially from the Santa Marta area northwards in N Colombia and along the coastal plain of Venezuela. At least 25-30% of the specimens of *subrufescens*, even from the dry Santa Marta area, cannot be distinguished reliably from those of *reconditus* and less than half of those from the Magdalena valley

are recognizably distinct: variation appears essentially clinal with no clear breaks or "steps". The primary songs of all are indistinguishable (on the basis of the small samples available to me). I therefore recommend lumping *conexus* (with *reconditus*) into *subrufescens*. This situation resembles that in *Thamnophilus atrinucha* as described by Isler et al. (1998), who demonstrated a cline in darkness of ventral coloration in parallel with changes in rainfall along the Magdalena valley and recommended lumping the paler race *subcinereus* into *atrinucha* because it was impossible to specify its distributional limits objectively.

Regarding other described races, *spatha* of the moist Serranía de Macuira at the tip of the desertic Guajira Peninsula is notably paler than any specimens I have seen of *subrufescens*. I have only seen two specimens of this subspecies but they do indeed seem diagnosably different. In one sense, this form represents simply the dry extreme of Gloger's rule (reviewed by Zink and Remsen 1986), being much the palest of the entire *subrufescens* group, but in this case it appears to be quite isolated from *subrufescens* from around the base of the Sierra Nevada de Santa Marta by ca. 100 km of open desert unsuitable for motmots. If only because both its range and its coloration seem discretely different, I will continue to recognize *spatha* as a distinct subspecies.

Second, *osgoodi* is also recognizable on the basis of its very rufescent coloration over the underparts, as well as its apparently different primary song (though again, sample sizes are small). This form is essentially isolated from *subrufescens* in the wet lowlands and foothills around the southern and eastern shores of the Lago de Maracaibo, including Norte de Santander in Colombia (although some gene flow may occur; see above). A number of other races of various taxa are similarly isolated by the very dry coastal lowlands of N Venezuela and the mountains of the Serranía de Perijá and the Mérida Andes from the lowlands to the north, south and west. Some individuals (ca. 10%) of *osgoodi* show a greenish wash across the breast and so resemble some individuals of "*reconditus*", but are mostly darker than adjacent populations of

subrufescens and usually show more purple feathers in the posterior diadem and around the mask than the latter.

As mentioned above, *argenticinctus* of SW Ecuador and extreme NW Peru is also clearly a distinct subspecies. It differs from *subrufescens* on average in being considerably greener, though some individuals from the Magdalena valley (including the type of *olivaresi*) are as green; it also differs in details of the color of the diadem, although this distinction is not wholly clear-cut. Ridgely & Greenfield (2001) suggested that *argenticinctus* might best be treated as a separate species, but I find the basis for this to be much less solid than for *bahamensis*: it is much more similar to the greener individuals of *subrufescens* in color and pattern and is essentially identical in biometrics. The latter point is important, since size (mass) and relative lengths of bills, wings and tails are quite constant among the members of the *subrufescens* group, with the sole exception of *bahamensis*. It appears to be isolated in the drier forests of the Tumbesian region, and it is interesting that in its greenness it recalls some birds from the drier parts of the Magdalena valley. Its single-hoot song may also be diagnosably different, but a better sample will be required to document this.

Finally, I will enter into greater detail in the case of *olivaresi*, because its affinities have been misinterpreted in two recent important publications (Snow 2000, Restall et al. 2006). This form was described by Hernández & Romero (1978) from two specimens, and its distribution was considered to comprise "the upper valley of the Río Chicamocha and its affluents", which constitutes a dry, rain-shadow enclave in the western slope of the Eastern Andes and includes endemic subspecies of several other taxa, plus the endemic species *Amazilia castaneiventris* (Chestnut-bellied Hummingbird) and *Thryothorus nicefori* (Nicéforo's Wren). I have examined the type (ICN 11100 from Soatá, Boyacá) and paratype (ICN 17461 from the Mesa de los Santos, Santander in the watershed of the Río Suárez, an affluent of the Río Chicamocha). The describers distinguished *olivaresi* from *subrufescens* of the Magdalena

valley (into which the Chicamocha flows) on the basis of its much more greenish coloration on the throat, chest, belly and back; from *spatha* by its darker, duller mantle and more greenish breast; and from *osgoodi* by its much less rufescent tones below, especially on the throat and chest. Perhaps because of the greenness of its plumage, Snow (2000) included *olivaresi* in his "*momota* group" rather than with *subrufescens* and allies, in spite of the statements of the describers to the effect that it was evidently a derivative of *subrufescens*; this determination was followed by Restall et al. (2006), and the plate in the latter work shows *olivaresi* as a much larger, greener bird than is actually the case: clearly the relevant specimens were not examined by these authors.

The two specimens of *olivaresi* are indeed decidedly greener than most specimens of *subrufescens*, but the range of variation in this form was not adequately taken into account by either the describers of *olivaresi* or by subsequent authors. In the large series of *subrufescens* in the AMNH from Bonda (the type locality) are two specimens that answer quite well to the description and features of *olivaresi* as well as several others that approach it in coloration (cf. Fig. 5); and in the ICN collection is a specimen from Beltrán in S Cundinamarca (ICN 16697) that is at least as green as the type of *olivaresi* (and which, curiously, was included in *subrufescens* by the describers of *olivaresi* without comment). Ten other specimens in the ICN collection come from localities between those of *olivaresi* and Beltrán (which are separated by nearly 200 km), and are more ochraceous below (as are most specimens of *subrufescens*). Moreover, I have observed individuals of *Momotus* in both the Chicamocha and Suárez valleys (including at the type locality of *olivaresi*) that are typical of *subrufescens* in the degree of ochraceous tones below – and which were singing the typical one-hoot songs of the *subrufescens* group. The measurements of the type and paratype of *olivaresi* also fall well within the ranges of measurements of *subrufescens* from the Magdalena valley. Hence, I conclude that *olivaresi* is not distinguishable from *subrufescens* and should be considered synonymous with it. Moreover, the wing and tail measurements of *olivaresi* are well outside the

ranges for *microstephanus* of the "*momota* group". In all plumage patterns of the diadem, mask and racquets the *olivaresi* specimens are perfectly typical of *subrufescens* and its allies, not the cisandean *microstephanus* or *momota:* I find no discernable basis for the inclusion of "*olivaresi*" in the cis-Andean *momota* group, *contra* Snow (2000) and Restall et al. (2006).

To summarize, I recommend that the number of subspecies of *subrufescens* be reduced to four: *subrufescens*, *spatha, osgoodi* and *argenticinctus.* These four allopatric and diagnosable forms might be recognized as species under the phylogenetic species definition, but because the differences seem not to be of the kind or magnitude likely to promote reproductive isolation, I consider that they are best treated as subspecies.

TAXONOMIC CONCLUSIONS.-   Based on my analyses of plumage, biometrics and voice, I recommend that the "*Momotus momota* complex" in the area between southern Middle America, Trinidad and northern Peru be divided into five species-level taxa, which with their included subspecies should be treated as follows:

Momotus lessonii Lesson 1842.   Included subspecies: nominate, *goldmani* Nelson 1900, *exiguus* Ridgway 1912. S Mexico to NW Panama. The status of *coeruliceps* (Gould 1836) of NE Mexico as a separate species is beyond the scope of this study, but I note that if it be deemed only subspecifically distinct, the species should be called *coeruliceps* as this name has priority.

Momotus aequatorialis Gould 1858.   Included subspecies: nominate, *chlorolaemus* Berlepsch and Stolzmann 1902. The Andes from NC Colombia to NE Bolivia.

Momotus subrufescens Sclater 1853.   Included subspecies: nominate (synonyms: *conexus* Thayer & Bangs 1906, *reconditus* Nelson 1912, *olivaresi* Hernández & Romero 1978), *osgoodi* Cory 1913, *argenticinctus* Sharpe 1892, *spatha* Wetmore 1946. C Panama to NC Venezuela and the Magdalena valley of Colombia; SE Ecuador and extreme NW Peru.

Momotus bahamensis (Swainson 1837). Note that if considered conspecific with *subrufescens,* the species name would be *bahamensis.* Trinidad and Tobago.

Momotus momota (Linnaeus 1766). Included subspecies: nominate, *microstephanus* Sclater 1857 and the following beyond the area of this study: *ignobilis* Berlepsch 1889, *marcgravianus* Pinto & Camargo 1961, *nattereri* Sclater 1857, *simplex* Chapman 1923, *pilcomajensis* Reichenow 1919, *cametensis* Snethlage 1912, and *paraensis* Sharpe 1892. Venezuela (S of the Orinoco) and the Guianas S through the entire Amazon basin to extreme N Argentina and Paraguay. The extralimital part of the complex most requires further analysis as several of the included forms differ strikingly in size and coloration; I am not aware of vocal data for most of these.

ENGLISH NAMES.- The inclusive name for the *M. momota* complex as a whole has long been "Blue-crowned Motmot". I suggest that this name be restricted to the Mexican form *coeruleiceps* should this be considered a species apart; if it were to include *lessonii* this name could apply to the broader species. If *lessonii* were to be considered a species distinct from *coeruleiceps*, I suggest Skutch's (1964) name Blue-diademed Motmot (originally coined for this form, though occasionally applied more widely since all of the taxa considered here have blue diadems but not blue crowns). For *subrufescens* and allies I suggest the name Whooping Motmot, because the one-hoot song (which does indeed sound more like a whoop) is the most striking single feature that separates this group from all other taxa. For *bahamensis* the obvious name would be Trinidad Motmot. For *M. momota* itself, I suggest Amazonian Motmot since the Amazon basin includes the bulk of its distribution, and because due to the great degree of variation of size, pattern and color among its different named subspecies, I can devise no sufficiently inclusive, appropriate name based upon morphology or appearance. Finally, although *aequatorialis* already has received the name Highland Motmot in several recent publications, I would suggest that Andean Motmot is more appropriate because several Middle American taxa are also highland birds.

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Appendix 1. Recordings of members of the *Momotus momota* complex analyzed in this study.

Taxon	Catalog no.[1]	Locality	Elev	Recordist	No. Inds.
lessonii	F1049/2	Costa Rica: Provincia San José: Montes de Oca, Monterrey	1275	F. G. Stiles	1
"	F871	Costa Rica: Provincia San José: San Pedro, U. de Costa Rica	1200	F. G. Stiles	1
"	F591	Costa Rica: Puntarenas: Las Cruces	1200	J. W. Hardy	1
"	F584	Costa Rica: Puntarenas: Monteverde	1300	J. W. Hardy	1
"	F51	Nicaragua: Matagalpa: Santa María de Ostuma	1100	J. W. Hardy	1
conexus	F1849/1	Panama: Panama: Parque Nacional Soberanía: Pipeline Road	100	E. S. Morton	1
"	F849	Panamá: Panamá: Parque Nacional Soberanía: Pipeline Rd.	100	D. Mann	1
reconditus	F1347/10	Colombia: Chocó: Sautatá	50	F. G. Stiles	1
"	H10598	Colombia: Chocó: PNN Los Katios	50	F. G. Stiles	1
subrufescens	C65031	Venezuela: Lara: Pie de Cocota: Boraure	430	P. W. Schwartz	1
"	C65032	Venezuela: Lara: Licua, Las Cocuizas	nd	P. W. Schwartz	1
"	H4491	Colombia:Tolima:Armero:Hda. Cardonal	550	M. Alvarez R.	1
"	H4931	Colombia: Bolívar: Sn.Juan Nepumoceno:SFF Los Colorados	300	M. Alvarez R.	1
"	H4665	Colombia: Bolívar: Zambrano		M. Alvarez R.	1
"	H9584	Colombia: Cesar: Valledupar: Reserva Natural Los Besotes	500	M. Alvarez R.	1
"	H9586	Colombia: Cesar: Valledupar: Reserva Natural Los Besotes	500	M. Alvarez R.	1
"	FGS C-15	Colombia:Santander: Sabana de Torres: Res.Cabildo Verde	160	F. G. Stiles	2
osgoodi	C65017	Venezuela: Zulia: Río Arcuaiza	35	P. W. Schwartz	1
"	C65018	Venezuela: Zulia: Alto de Cedro 1	50	P. W. Schwartz	1
"	C65019	Venezuela: Zulia: Alto del Cedro 2	50	P. W. Schwartz	1
"	C65033	Venezuela:Zulia:km 9 of road to Rio de Oro (Catatumbo)	60	P. W. Schwartz	1
argenticinctus	C57050	Ecuador: Loja: Catacocha	1550	M. B. Robbins	2
"	C122715	Ecuador: Guayas: Guayaquil	140	L. R. Macaulay	1
"	KB127	Ecuador: Manabí: Zamia Trail	500	K. S. Berg	1
bahamensis	AJ1	Trinidad:Arima Valley: Asa Wright Nature Center	400	A. Jaramillo	2
"	AJ2	Trinidad:Arima Valley: Asa Wright Nature Center	400	A. Jaramillo	1
"	AJ3	Trinidad:Arima Valley: below Asa Wright Nature Center	300	A. Jaramillo	1
"	AJ4	Tobago: Main Ridge Forest Reserve	150	A. Jaramillo	2
"	C6638	Trinidad: Arima Valley: St. Patrick´s Estate	nd	D. W. Snow	1
microstephanus	H1650	Colombia: Caquetá:Solano: PNN Chiribiquete: Río Mesay	ca. 330	M. Alvarez R.	1
microstephanus	H1732	Colombia: Caquetá:Solano: PNN Chiribiquete: Río Mesay	ca. 330	M. Alvarez R.	1
"	H3119	Colombia: Caquetá:Solano: PNN Chiribiquete: Río Mesay	ca. 330	M. Alvarez R.	2

Continuation Appendix 1. Recordings of members of the *Momotus momota* complex analyzed in this study.

Taxon	Catalog no.[1]	Locality	Elev	Recordist	No. Inds.
"	H3376	Colombia: Caquetá:Solano: PNN Chiribiquete: Cuñaré	ca. 330	M. Alvarez R.	1
"	H3412	Colombia: Caquetá:Solano: PNN Chiribiquete: Cuñaré	ca. 330	M. Alvarez R.	1
"	H3774	Colombia: Caquetá:Solano: PNN Chiribiquete: Mesay Alto	ca. 350	M. Alvarez R.	1
"	H3777	Colombia: Caquetá:Solano: PNN Chiribiquete: Mesay Alto	ca. 350	M. Alvarez R.	1
"	H5340	Colombia: Caquetá:Solano: PNN Chiribiquete: Cuñaré-Amú	ca. 330	M. Alvarez R.	1
"	H6072	Colombia: Caquetá:Solano: PNN Chiribiquete: Cuñaré-Amú	ca. 330	M. Alvarez R.	1
"	H9749	Colombia: Meta: Río Duda	500	M. Alvarez R.	1
"	FGS C-14	Colombia: Meta: San Martín: Caño Camoa	450	F. G. Stiles	2
"	H11300	Colombia: Amazonas: Leticia, Monilla Amena	100	F. G. Stiles	1
"	C65026	Venezuela: Apure: El Nula	260	P. W. Schwartz	1
"	C65027	Venezuela: Apure: El Nula	260	P. W. Schwartz	1
"	C18089	Ecuador: Napo-Pastaza: Limoncocha	100	J. P. O'Neill	1
"	C18086	Ecuador: Napo-Pastaza: Limoncocha	100	J. P. O'Neill	1
"	F1572	Perú: Loreto: Las Cruces	nd	B. Coffey	1
"	F1586	Perú: Loreto: Pucallpa: Yarinacocha	nd	"	1
momota	C72448	Guyana:Kanuku Mts.:Maipaima Creek	104	D.W. Finch	1
"	C106320	Guyana:left bank of Kuyuwini River	245	"	1
aequatorialis	H8030	Colombia:Caldas:Aranzazu:Hda. Termópila	2250	S. Córdoba	1
"	H8099	Colombia:Caldas:Aranzazu:Hda. Termópila	2250	S. Córdoba	1
"	H10552	Colombia:Caldas:Filadelfía:Bosque Samaria	1900	"	1
"	H11935	Colombia:Valle del Cauca:Yotoco:Reserva Yotoco	1450	J. A. López	1
"	H11954	Colombia:Valle del Cauca:Yotoco:Reserva Yotoco	1600	J. A. López	1
"	H12223	Colombia:Valle del Cauca:Yotoco:Reserva Yotoco	1500	J. A. López	1
"	H15363	Colombia:Risaralda:Sta. Rosa de Ca-bal:Pque.Mpal.Campoalegre	2380	S. Córdoba	1
"	H15364	Colombia:Risaralda:Sta. Rosa de Ca-bal:Pque.Mpal.Campoalegre	2400	"	1
chlorolaemus	C17618	Peru:Cuzco:S Of Huyro:Bosque Aputinye	1675	T.A.Parker	1
"	C40103	Peru, Pasco, Playa Pampa, on Pozuzo-Panao trail	2000	T.S. Schulenberg	1

[1]Abbreviations of sound archives and collections of recordings: AJ: recordings by Alvaro Jaramillo; C: Macaulay Natural Sounds Archives, Cornell University; F: Florida State Museum, Natural Sounds Library, University of Florida; FGS: recordings of F. G. Stiles; H: Banco de Sonidos de Animales, Instituto Alexander von Humboldt, Villa de Leyva, Colombia; KSB: recordings by Karl S. Berg.

Appendix 2. Plumage descriptions of focal taxa in the "*Momotus momota* complex".

The following descriptions refer to adults (no sexual dichromatism was noted); young birds were generally easy to distinguish because the black of the mask and crown was usually dingy, the inner edge of the diadem was not clean-cut as in adults but diffuse with the feathers of the crown often tinged or bordered with dull blue or turquoise to mostly blue; the ventral feathers were fluffier and usually duller in hue, often decidedly dusky on the abdomen. In some juveniles, the bill was also decidedly smaller than in adults.

1. *lessonii*: this form is notably variable in the color of the underparts, with less individual variation in other parts of the plumage.

UNDERPARTS: Throat usually green, often decidedly washed with blue and contrasting with chest. Chest usually olive to ochraceous-olive, in some approaching dull rufous; abdomen similar but washed with green to bluish-green, thus chest is the least green in hue. In general, the rufous-to-green variation below among individuals is quite pronounced, with most tending towards the rufous extreme. Thighs usually blue-green to green, not contrasting strongly with the abdomen. The longer feathers of the black pectoral "stickpin" show very narrow, inconspicuous turquoise borders.

BORDER OF MASK: A: light blue, usually narrow but in a few broader and more conspicuous; B1: inconspicuous, usually a few blue feathers not contrasting strongly, especially in individuals with the most bluish throats; B2: pale blue to turquoise, usually a fairly well-defined line brighter than and contrasting with throat; a minority have some violet feathers mixed in, especially anteriorly; B3: no border in most; a few have 1-3 blue feathers.

DIADEM: Anterior portion (above forehead) pale blue, narrow to quite broad, this color extending back to above the eye; the posterior portion darker blue with varying amounts of violet mixed in along the posterior border; in a few the posterior portion is mostly violet with only a narrow border of blue adjoining the crown. The black medial portion of the crown is typically solid black, more extensively so than in *aequatorialis*. As in the latter, the diadem is bordered posteriorly by a well-defined band of black that extends back from behind each eye. A few individuals have a small area of rusty feathers concealed beneath the occipital portion of the diadem, but most have none.

UPPERPARTS: Nape and hindneck olive green, often more or less washed with tawny or ochraceous; mantle green, uniform to brightest on wing-coverts.

RACQUETS: Blue, shading gradually to blackish on the distal ¼ to ½ and decidedly longer than wide.

2. *conexus*

UNDERPARTS: Throat bright olive-green to green, sometimes tinged with bluish; breast varies from rather bright olive-green to ochraceous-olive, sometimes with a cinnamon-rufous tinge; belly cinnamon-buff, ochraceous-tawny to rather pale rufous; thighs usually green to olive-green, offering moderate contrast with the more ochraceous to cinnamon flanks and abdomen. Individual variation in the rufous-to-green hues below is very pronounced, but the chest is typically slightly to distinctly greener than the belly. The turquoise borders on the longer black "stickpin" feathers usually narrow but more conspicuous than in *lessonii*.

BORDER OF MASK: A: usually narrow and inconspicuous, pale turquoise to blue, sometimes absent; B1: usually inconspicuous, limited to a few blue or turquoise feathers; B2: usually conspicuous, with blue, turquoise and violet feathers in varying proportions; all three colors usually present; B3: border absent or limited to a few (<5) turquoise or blue feathers.

DIADEM: Anterior portion broadest, pale turquoise, the feathers with bases and along shaft usually dull cinnamon to rusty, giving a "soiled" or "stained" look to varying degrees; the lateral portion of the diadem much narrower and a somewhat darker sky blue; the posterior portion broader (but less so than the anterior portion), mostly or entirely violet, the feathers with dusky bases, a blue medial portion (sometimes absent), and the distal half or more violet. In a few, some of the longest, most posterior feathers have inconspicuous black tips. In most, there is a rufous area concealed beneath the occipital portion of the diadem, but in a few, this area is visible, occasionally spreading onto the upper nape. The black central portion of the crown occasionally includes a few scattered turquoise feathers.

UPPERPARTS: Nape and sides of neck olive green, usually more or less strongly washed with ochraceous that often extends onto the upper back. Lower back, rump, tail-coverts green, wing-coverts brighter green; base of tail green to blue-green, shading to blue distally.

RACQUETS: Blue, passing abruptly to black over the distal ¼ to ½; the transition more sharply defined than in *lessonii*. The racquets are also noticeably broader, more spatulate in shape and usually more conspicuous in this species than in *lessonii*.

3. *reconditus*

UNDERPARTS: Throat bright to rather dark olive to olive-green, sometimes with a bluish wash; chest typically dark olive, often washed with rufous-ochre; belly dull cinnamon-rufous to dark rufous, averaging considerably darker than that of *conexus*; a few have the abdomen decidedly greener, with only a dark rufous wash, showing little contrast with the chest. Thighs olive-green to green, contrasting fairly strongly with the rufous or olive-rufous flanks. The black pectoral spot is similar to that of *conexus*.

BORDER OF MASK: A: narrow, usually with somewhat darker blue (less turquoise) feathers than in *conexus*; rarely absent; B1: usually inconspicuous, with no more than 2-3 blue feathers; B2: broad and conspicuous with blue, turquoise and violet feathers present, averaging more extensively violet than in *conexus*; B3: absent or with only 1-3 blue (usually) or violet feathers:.

DIADEM: Anterior portion broadest, turquoise to pale blue, the feathers with rusty to clay-colored bases that often show through, giving a "soiled" look much as in *conexus*; the middle (supraocular) portion narrowest, darker blue; the posterior (occipital) portion broader, mostly violet with some blue to blue-green mixed in, especially along the border of the black crown; some of the violet feathers of the posterior border may have narrow black tips, much as in *conexus*. Most birds have a

Continuation Appendix 2. Plumage descriptions of focal taxa in the "*Momotus momota* complex".

more or less concealed rufous area underlying the occipital portion of the diadem. The crown is black, similar in extent to that of *conexus*, occasionally with a few scattered blue-green to turquoise feathers.

UPPERPARTS: Nape and hindneck with olive to rufous wash that may continue onto the upper back; lower back, rump, tail-coverts and base of tail green, brighter green on wing-coverts, overall dorsal coloration similar in hue or slightly darker than that of *conexus*.

RACQUETS: In form like those of *conexus*; blue basally, passing abruptly to black on distal 1/3 to ½ or more; black averaging more extensive than in *conexus*.

4. *subrufescens*: Averaging paler than either of the two preceding forms but very variable; intergrades with *reconditus* over a rather broad area of NE Antioquia, S Córdoba and W Sucre in NW Colombia; the birds from the middle and upper Magdalena valley average somewhat darker than those from the northern coastal plain, and in fact are virtually indistinguishable from most *conexus*. (Indeed, Meyer de Schauensee (1948-52) cited a *conexus*-like specimen from NW Colombia as a "connecting link" with that form to justify placing these birds with *conexus*, but see below). Birds from the N coastal region of Venezuela are similar in color to those of the northern coastal plain of Colombia.

UNDERPARTS: Throat bright olive-green to green, sometimes tinged with bluish; breast varies from pale to fairly dark olive-green to olive-ochraceous, sometimes with a rather faint rufous wash; belly deep buff, cinnamon-buff, tawny to pale or dull rufous; thighs usually green to olive-green occasionally blue-green, contrasting with the more ochraceous to cinnamon flanks. As in the two preceding forms, the throat is greenest and the chest is usually decidedly greener than the abdomen; the pectoral spot is also similar, the turquoise borders of the longer feathers often quite broad and conspicuous. The type of *olivaresi* is an extremely green bird with a strongly bluish throat and the abdomen olive green with a rusty wash. I will discuss this form in more detail below; suffice it to say here that I consider it to represent merely the green extreme of variation within *subrufescens*.

BORDER OF MASK: A: usually narrow and inconspicuous, pale turquoise to pale blue, sometimes absent; B1: usually inconspicuous, limited to a few turquoise or blue feathers; B2: broader, usually conspicuous, with varying proportions of blue, turquoise and violet feathers with all three colors usually present; B3: border absent or limited to a few (<5) turquoise or blue feathers.

DIADEM: Anterior portion broadest, pale silvery turquoise, the rusty to clay-colored bases and shafts of the feathers giving a "soiled" look that is sometimes more prominent in this form than in *conexus* or *reconditus*. Lateral (supraorbital) portion narrowest and sky-blue, the posterior (occipital) portion broader, mostly violet except the portion adjoining the crown more or less mixed with blue (the feathers here with more or less blue medially, violet distally); a few feathers along the posterior border with narrow black tips. In most, a rufous area is concealed beneath the occipital portion of the diadem; in a few, the rufous spreads visibly onto the upper nape. The crown is black, occasionally with a few scattered turquoise feathers.

UPPERPARTS: Most like *conexus* in general: nape and sides of neck olive green, usually more or less strongly washed with ochraceous or tawny that often extends onto the upper back; rest of upperparts green, brightest on the wing-coverts; tail shades through blue-green to blue distally.

RACQUETS: Broad and spatulate as in the preceding three taxa; blue basally, passing abruptly to black on distal ¼ to ½ or more, similar to racquets of the preceding two forms.

4a. *spatha*: I have seen only two male specimens of this form, whose distribution appears restricted to one small range of low mountains at the tip of the Guajira Peninsula of extreme N Colombia.. The flat desert regions between its range and the nearest populations of *subrufescens* near Santa Marta are unsuitable for motmots. As might be expected, *spatha* closely resembles *subrufescens* in pattern, differing mainly in its decidedly paler coloration, especially below where the abdomen is a pale ochraceous-buff, the chest a pale olive, the throat pale green. I will not discuss this form further for lack of material.

5. *osgoodi*: This form is much more rufescent below than *subrufescens*, averaging more uniformly so than *reconditus* (in particular, the throat and chest are usually much less strongly greenish in hue) although a few individuals of these two taxa are quite similar.

UNDERPARTS: Throat dark rufous, washed with olive green in about half the individuals seen; in a few, the throat includes some brighter green feathers; chest dark rufous with definite dull olive wash in most; belly dark rufous; thighs green, olive-green to tawny-olive, contrasting moderately with the mostly tawny flanks. The pectoral "stickpin" is similar to that of *reconditus* and *conexus* in particular.

BORDER OF MASK: A: absent or narrow and inconspicuous (1-2 turquoise feathers, often with violet tips); B1: Usually inconspicuous, with 1-3 green to turquoise feathers, or absent; B2: a narrow to fairly conspicuous border, usually mostly or entirely violet; sometimes the bases of these feathers are blue, the tips violet, or the anterior feathers are mostly blue; B3: usually absent, at most a few blue or violet feathers, inconspicuous.

DIADEM: Anterior portion broadest, pale turquoise to blue with a strong rusty to rufous suffusion in the feather bases that is often much more extensive than in previous forms, in some nearly or quite blotting out the turquoise medially (on the forehead-forecrown); lateral portion sky-blue and narrow; posterior portion broader, mostly or entirely violet: the blue, when present, confined to the bases of the anterior feathers adjoining the crown; the occipital feathers sometimes with narrow black tips; crown black, occasionally with one or a few turquoise feathers. In most, a concealed patch of rufous beneath the occipital feathers that in a few spreads visibly onto the upper nape.

UPPERPARTS: Most birds have a strong rufescent wash on the sides and rear of the neck that usually extends onto at least the upper back; remaining upperparts green, averaging darker than those of *conexus* or *subrufescens*; tail green at base, shading to blue distally.

RACQUETS: Blue basally, passing abruptly to black on distal ¼ to ½ or more, similar to racquets of the preceding three taxa in

Continuation Appendix 2. Plumage descriptions of focal taxa in the "*Momotus momota* complex".

color and shape.

6. *bahamensis*: This form is most like *osgoodi* but is even more deeply and uniformly rufous below (the rufous approaching chestnut-rufous) and differs from all other members of the complex in the extensive blue areas around the mask.

UNDERPARTS: Throat deep, intense rufous; breast slightly paler and often with a faint olive-green wash, at least laterally; abdomen rufous, about as dark as the breast or slightly paler and without any olive wash; the flanks are typically washed with olive, the thighs green to blue-green contrasting sharply with the flanks and abdomen. The turquoise borders of the black pectoral feathers are usually broad and conspicuous.

BORDER OF MASK: A: usually a conspicuous blue to turquoise border that diffuses posteriorly, nearly or quite reaching the black border of the diadem and shading off to green posteriorly; B1: Usually one or a few blue or turquoise feathers, not very conspicuous; B2: a conspicuous border, the feathers mostly violet with blue or turquoise bases; B3: a narrow turquoise border or none; overall, the blue area around and above the mask is more extensive and diffuse than in any other form.

DIADEM: Anterior portion much the broadest, often extending to mid-crown, pale turquoise to sky blue, the feathers with rusty to brownish-buff bases that usually show through imparting a "soiled" look, sometimes the medial feathers extensively rufous; lateral portion darker blue, narrow; the blue continues posteriorly around the edge of the black center of the crown as a broad to narrow line that may disappear on the hindcrown; from the eye backwards the outer portion of the diadem is violet, the hindmost portion often entirely so. In most, a narrow band of black forms a posterior border to the diadem albeit often at least partly concealed beneath the violet. A rufous area is usually present but concealed beneath the occipital feathers of the diadem. A few blue or turquoise feathers are sometimes present in the black area of the crown.

UPPERPARTS: Most birds show a rufous wash across the nape, typically faint but in a few, conspicuous. Remaining upperparts green, palest and brightest on the wing-coverts; tail green basally, shading to rather dark blue distally.

RACQUETS: Basally dark blue, passing abruptly to black on distal ¼ to 1/3, similar to those of the preceding several taxa.

7. *argenticinctus*: The overall pattern of this isolated form resembles most closely that of *subrufescens* or *conexus* although it averages greener below, some birds approaching the "*olivaresi*" type; the main difference lies in the more extensive blue on the posterior diadem, with a more conspicuous and complete black border.

UNDERPARTS: Throat green to blue-green, usually strongly washed with blue (in a few, the blue is confined to the chin), the feathers with pale buffy bases; breast olive-green to ochraceous-olive, shading to tawny-buff or ochraceous-buff on the belly, sometimes approaching pale rufous; thighs typically green to olive-green, sometimes tinged blue, contrasting moderately with the more ochraceous flanks. The throat is typically the greenest, the belly the least green area of the underparts. The black "stickpin" resembles that of *conexus, reconditus* and *subrufescens.*

BORDER OF MASK: A: usually narrow, a few turquoise feathers forming a rather inconspicuous border to the posterior portion; B1: Absent or at best very inconspicuous, at most a few blue feathers offering little contrast with the throat; B2: narrow to quite broad, the feathers turquoise anteriorly and closest to the mask, more or less violet distally and posteriorly; B3: usually absent, occasionally 1-3 blue or violet feathers.

DIADEM: Anterior portion broadest, turquoise to sky blue; the feathers with brownish-buff bases that may show through, especially on the most turquoise-feathered birds, but rarely as conspicuously so as in *conexus* or *subrufescens.* The blue or turquoise of the forehead continues narrowly back over the eye and more broadly as a band around the posterior edge of the crown that is usually of constant width and at least as broad as the violet band along the posterior or peripheral portion of this part of the diadem; in a few the blue is reduced to a narrow line adjoining the crown, but in others the violet area is reduced to a narrow band along the posterior border. A narrow band of black subtends the diadem behind the eye, continuing around the rear edge of the diadem; in most this border is at least partly concealed but in a few it is complete; a concealed area of rufous occurs on the occiput of most individuals.

UPPERPARTS: many individuals show a definite ochraceous wash across the olive-green nape; the rest of the upperparts are fairly uniform green, dullest and most olive on the back and brightest on the wing-coverts; a few birds, usually those with the bluest throats, have a bluish tinge throughout; the tail shades to blue distally.

RACQUETS: Basally blue, the distal ¼ to ½ abruptly black; broad and spatulate.

8. *microstephanus*

UNDERPARTS: Throat typically olive-green to green with an olive wash; chest olive, more or less washed with rusty to ochraceous, most strongly on sides of neck; abdomen relatively pure green with little or no olive or rusty wash, thus greener than chest and, usually, throat; flanks more olive-green, often tinged with ochraceous or tawny; often a small area of dull buff in center of lower abdomen; thighs green to olive-green, contrasting little with flanks. Overall, the range of individual variation in colors below is much less than in most of the preceding forms, the most rufescent birds distinctly greenish-olive at least on the abdomen, the greenest birds with at least a tinge of ochraceous on the foreneck. The black feathers of the "stickpin" average less conspicuously bordered with turquoise than most of the preceding forms.

BORDER OF MASK: A: usually fairly broad and conspicuous, turquoise to sky blue; B1: usually fairly broad and conspicuous, sky blue to turquoise and contrasting with the duller, more olive throat; B2: similar in width or narrower, usually mixed blue and violet; B3: absent or narrow; when present, violet mixed with blue or wholly violet.

DIADEM: Anterior portion sky blue to turquoise (less pale and silvery than most previous forms) with little or no rusty to brownish in the feather bases; the middle (supraorbital) portion narrower, usually darker blue and often with some violet; the posterior portion broader (usually broader than the anterior portion), violet mixed with blue to entirely violet; frequently a small rufous area on upper nape, sometimes partly concealed by the posterior diadem, sometimes lacking but occasionally more extensive

Continuation Appendix 2. Plumage descriptions of focal taxa in the "*Momotus momota* complex".

and conspicuous.

UPPERPARTS: The ochraceous tinge of the sides of the breast often continues around the nape; the back is rather dull green, the remaining upperparts brighter green; the tail is green at the base, shading to blue distally.

RACQUETS: Blue, with an indistinct dusky to blackish border distally that occupies no more than ca. ¼ of the racquet, which is also less broad and spatulate than those of the preceding seven taxa.

9. momota: Overall, this form is very similar to *microstephanus* in color and pattern, so much so as scarcely to warrant a detailed description. The main difference is that the rufous area on the nape is usually much more extensive and conspicuous; also, the underparts of some birds attain more ochraceous to rufescent tones than in *microstephanus*, although most are indistinguishable in this feature.

10*. aequatorialis*: The amount of individual variation in coloration in this form is still less than that seen in *microstephanus*, with virtually all birds being decidedly green overall. Examples of this race from Ecuador are indistinguishable in color and pattern from those from Colombia. Birds of the race *chlorolaemus* from N Peru are essentially identical in pattern and only average slightly greener in hue.

UNDERPARTS: Throat green, often slightly to strongly washed with blue; breast green more or less washed with ochraceous-olive, this color usually fainter or absent on the belly, which in most is clear green; some individuals are nearly uniform green below. The black feathers of the pectoral "stickpin" have narrow, often inconspicuous turquoise borders.

BORDER OF MASK: A: always present, sharply defined and usually broad, pale blue or turquoise; much the most conspicuous portion of the border, the opposite of most other forms; B1: usually absent, at most with 1-3 blue feathers, inconspicuous; B2: usually a few bright blue or turquoise feathers, but much less conspicuous than in any of the preceding forms; B3: nearly always absent, at most 1-2 bright blue feathers; in general, the lower border of the mask is very poorly developed.

DIADEM: The black of the anterior forehead and nasal area is typically less extensive than in other forms, such that the anterior diadem usually reaches the base of the culmen. Anterior and lateral portions bright turquoise blue, sometimes passing to a slightly purer blue posteriorly, the posterior part usually with a narrow peripheral band or admixture of violet, sometimes only a violet tinge to the tips of the outermost feathers. From the eye back, a band of black completely encircles the diadem; only rarely is a small brownish area present on the occiput, invariably concealed beneath the posterior diadem. The crown is black, sometimes a few feathers with blue borders.

UPPERPARTS: The sides of the neck and hindneck are green, rarely with a faint ochraceous wash; the mantle is rather dark green, brightest on the wing-coverts; the tail is rather dark green basally, passing to blue distally.

RACQUETS: Blue, often tinged dark green laterally; at most an indistinct, very narrow dusky border at the tip. The racquets of this form are also relatively narrower and less conspicuous than those of the other taxa studied.

Appendix 3. Distribution of green vs. ochraceous-olive colors on the chest vs. lower breast-abdomen in members of the *Momotus momota* complex in southern Central and northern South America.

Subspecies	Color of chest in relation to that of lower breast-abdomen:					N	Mean score
	conspicuously greener (1)	slightly greener (2)	approximately concolor (3)	slightly more ochraceous (4)	conspicuously more ochre (5)		
lessonii	0	0	6	8	1	15	3.67
conexus	4	9	2	0	0	15	1.92
reconditus	10	15	2	0	0	27	1.70
subrufescens	18	53	6	0	0	77	1.84
osgoodi	0	9	6	0	0	15	2.40
bahamensis	0	7	8	0	0	15	2.53
argenticinctus	2	8	0	0	0	10	1.80
microstephanus	0	4	15	52	20	91	3.97
momota	0	0	3	13	10	26	4.27
aequatorialis	0	1	18	20	3	42	3.60

Appendix 4. Color of thighs vs. abdomen-flanks and contrast between the two in members of the *Momotus momota* complex in southern Central and northern South America.

	A. Color of thighs (tibiae)						
Subspecies	blue-green (1)	green (2)	olive green (3)	tawny olive (4)	tawny (5)	**N**	**Mean score**
lessonii	7	7	3	3	0	20	2.10
conexus	0	5	9	2	0	15	3.00
reconditus	1	5	7	2	1	16	2.81
subrufescens	1	11	21	10	3	46	3.06
osgoodi	1	3	4	6	1	15	3.20
bahamensis	18	4	0	0	0	22	1.18
argenticinctus	2	5	2	1	0	10	2.22
microstephanus	7	28	27	6	0	68	2.47
momota	3	9	6	0	0	18	2.17
aequatorialis	5	22	7	1	0	35	2.11

	B. Color of abdomen-flanks					Mean score	Contrast (diff. means)
lessonii	1	6	12	1	0	2.45	0.35
conexus	0	0	0	6	9	4.60	1.60
reconditus	0	0	0	6	10	4.62	1.81
subrufescens	0	0	2	16	27	4.46	1.40
osgoodi	0	0	2	2	11	4.60	1.40
bahamensis	0	0	0	7	15	4.68	3.50
argenticinctus	0	0	0	8	2	4.20	1.98
microstephanus	0	9	43	16	0	3.10	0.63
momota	0	0	3	10	5	3.11	0.94
aequatorialis	2	16	14	3	0	2.51	0.40

Appendix 5. Features of the pectoral "stickpin" in members of the *Momotus momota* complex in southern Central and northern South America.

	A. Number of black feathers (adults only)					
Subspecies	**1**	**2**	**3**	**4**	**5**	**Mean score**
lessonii	1	9	9	1	0	2.50
conexus	1	6	5	1	0	2.46
reconditus	0	11	7	1	0	2.47
subrufescens	0	20	18	2	0	2.38
osgoodi	2	5	8	0	0	2.40
bahamensis	2	11	6	1	0	2.30
argenticinctus	10	0	2	6	2	3.00
microstephanus	2	23	31	6	0	2.68
momota	1	4	9	3	1	2.94
aequatorialis	1	6	14	10	0	3.06

	B. Extent of turquoise border on longest feathers				
	none (0)	≤ ½ of border, narrow (1)	> ½ of border, narrow (2)	> ½ of border, broad (3)	**Mean score**	**N**
lessonii	0	14	6	0	1.30	20
conexus	0	1	9	3	2.15	13
reconditus	0	2	11	6	2.21	19
subrufescens	0	5	19	16	2.28	40
osgoodi	0	1	11	3	2.13	15
bahamensis	0	1	8	11	2.50	20
argenticinctus	0	1	6	3	2.20	10
microstephanus	2	20	3|1	9	1.76	62
momota	0	7	11	1	1.67	18
aequatorialis	2	13	15	1	1.48	31

Appendix 6. Colors of the anterior and posterior portions of the diadem in members of the *Momotus momota* complex in southern Central and northern South America.

	A. Anterior diadem (forecrown)					
Subspecies	entirely turquoise or sky-blue, no brownish (0)	clay-color or brownish in feather bases (1)	evident clay-color to rusty medially (2)	conspicuous clay-color to rufous medially (3)	**N**	**Mean score**
lessonii	13	2	0	0	15	0.13
conexus	0	4	9	2	15	1.87
reconditus	3	10	12	2	27	1.48
subrufescens	4	6	30	6	46	1.83
osgoodi	1	4	7	3	15	1.80
bahamensis	0	2	8	5	15	2.20
argenticinctus	1	4	5	0	10	1.40
microstephanus	26	32	0	0	58	0.55
momota	7	8	0	0	15	0.53
aequatorialis	33	7	0	0	40	0.17

	B. Posterior diadem (occipital portion)					
	entirely blue (0)	blue, some violet posteriorly (1)	amt. blue ≈ violet (2)	violet, some blue proximally (3)	entirely violet (4)	**Mean score**
lessonii	0	3	6	6	0	2.22
conexus	0	0	2	11	2	3.00
reconditus	0	0	5	20	2	2.89
subrufescens	0	0	9	26	11	3.04
osgoodi	0	0	1	8	6	3.30
bahamensis	0	0	0	6	9	3.60
argenticinctus	0	3	5	2	0	1.90
microstephanus	0	0	2	26	30	3.45
momota	0	1	2	6	6	3.13
aequatorialis	8	26	6	0	0	0.95

Appendix 7. Aspects of the form and pattern of the diadem in members of the *Momotus momota* complex in southern Central and northern South America.

	A. Relative widths of anterior and posterior portions of the diadem				
Subspecies	anterior > posterior (0)	anterior ≈ posterior (1)	anterior < posterior (2)	**N**	**Mean score**
lessonii	3	10	3	16	1.00
conexus	15	0	0	15	0.00
reconditus	24	1	0	25	0.04
subrufescens	39	1	0	40	0.02
osgoodi	14	1	0	15	0.07
bahamensis	15	0	0	15	0.00
argenticinctus	9	1	0	10	0.10
microstephanus	7	24	19	50	1.24
momota	2	9	4	15	1.13
aequatorialis	6	20	9	35	1.09

	B. Black border to posterior diadem (separating diadem from nape)			
	absent (0)	narrow, interrupted, not conspicuous (1)	complete, more or less conspicuous (2)	**Mean score**
lessonii	0	1	15	1.88
conexus	10	3	0	0.23
reconditus	17	8	0	0.32
subrufescens	27	13	0	0.32
osgoodi	12	3	0	0.20
bahamensis	2	10	3	1.07
argenticinctus	5	4	1	0.60
microstephanus	22	25	3	0.62
momota	5	10	0	0.67
aequatorialis	0	4	31	1.89

Appendix 8. Relative degree of development of different segments of the border of the mask (see Fig. 2) among members of the *Momotus momota* complex in southern Central and northern South America. Abbreviations: 0=no border - bright feathers absent; 1=inconspicuous - few bright feathers; 2=conspicuous - numerous bright, contrasting feathers.

		Mask border segments:											
		A			B1			B2			B3		
Subspecies	N	0	1	2	0	1	2	0	1	2	0	1	2
lessonii	15	0	7	8	13	2	0	0	7	8	14	1	0
means			1.53			0.13			1.53			0.07	
conexus	15	0	14	1	7	8	0	0	4	11	13	2	0
means			1.04			0.53			1.67			0.13	
reconditus	20	0	17	3	7	13	0	0	8	12	14	6	0
means			1.15			0.65			1.60			0.30	
subrufescens	30	2	27	1	15	15	0	0	7	23	25	5	0
means			0.97			0.50			1.77			0.17	
osgoodi	15	5	10	0	6	9	0	0	7	8	14	1	0
Means			0.67			0.60			1.53			0.07	
bahamensis	15	0	3	12	5	9	1	0	3	12	11	4	0
means			1.80			0.73			1.80			0.27	
argenticinctus	10	2	7	1	3	6	1	0	3	7	8	2	0
means			0.90			0.80			1.70			0.20	
microstephanus	41	2	33	6	4	26	11	2	29	10	39	2	0
means			1.10			1.17			1.20			0.05	
momota	12	0	9	3	1	8	3	0	9	3	11	1	0
means			1.20			1.17			1.20			0.08	
aequatorialis	32	0	7	25	28	4	0	16	16	0	30	2	0
means			1.78			0.12			0.50			0.06	

Appendix 9. Presence and extent of a rufous area on the occiput or nape in *Momotus* motmots of southern Central and northern South America.

Subspecies	N	No rufous present (0)	Rufous present, wholly concealed (1)	Inconspicuous, small rufous area visible (2)	Conspicuous, large rufous area visble (3)	Mean
lessoni	20	18	2	0	0	0.10
conexus	13	4	9	0	0	0.69
reconditus	15	4	10	1	0	0.80
subrufescens	32	7	22	3	0	0.87
osgoodi	12	2	7	3	0	1.08
bahamensis	22	2	17	3	0	1.05
argenticinctus	10	2	8	0	0	0.80
microstephanus	63	22	18	13	10	1.17
momota	45	1	2	6	36	2.71
aequatorialis	40	37	3	0	0	0.07

Appendix 10. Color and pattern of the racquets in members of the *Momotus momota* group in southern Central and northern South America.

		Black in distal part of racquet:				
Subspecies	N	Absent: entirely blue (0)	Blue, indistinct dusky border distally (<1/4)	Blue basally, distal 1/4-1/2 black	Blue basally, distal 1/2 or more black	Mean
lessonii	22	0	2	12	8	2.27
conexus	13	0	0	3	10	2.77
subrufescens	30	0	0	6	24	2.80
reconditus	20	0	0	5	15	2.75
osgoodi	15	0	0	7	8	2.53
bahamensis	17	0	0	9	8	2.47
argenticinctus	9	0	0	3	6	2.67
microstephanus	41	1	32	8	0	1.17
momota	14	0	10	4	0	1.29
aequatorialis	32	20	12	0	0	0.75

Appendix 11. Means (± 1 standard deviation) and ranges of measurements of *Momotus* taxa from northern South America and southern Central America. All linear measurements in mm; sample sizes in parentheses. Data for sexes presented separately except for body mass (g).

Taxon	Body Mass (g)	Sexo	Exposed Culmen	Total Culmen	Bill from Nostril	Bill depth at nostril	Closed Wing Chord	Tail length
Taxa and principal populations measured								
lessonii (S Central Amer.)	115.5 ± 11.4 (32) 90-135	M	37.65 ± 2.25 (25) 35.3-42.0	44.50 ± 2.47 (25) 40.6-50.5	29.48 ± 2.23 (25) 26.6-34.5	11.79 ± 0.59 (25) 10.3-12.9	136.79 ± 4.07 (24) 130.5-142.3	229.77 ± 8.23 (21) 215.0-245.0
		F	36.35 ± 1.90 (20) 33.7-39.8	43.33 ± 2.32 (20) 39.6-46.4	28.23 ± 1.82 (20) 25.5-33.1	11.37 ± 0.51 (20) 10.6-12.4	134.23 ± 3.05 (20) 128.4-140.0	224.95 ± 8.58 (18) 206.0-233.5
conexus (C Panama)	93.7 ± 3.3 (4) 89-99	M	36.53 ± 1.50 (23) 33.5-39.5	42.17 ± 1.34 (23) 39.8-44.3	29.73 ± 1.33 (23) 27.7-31.9	11.91 ± 0.38 (23) 11.2-12.9	125.04 ± 4.36 (23) 118.2-133.4	233.49 ± 9.16 (20) 211.5-246.5
		F	35.63 ± 1.89 (24) 32.0-39.2	41.15 ± 1.57 (24) 37.8-44.4	28.89 ± 1.61 (24) 25.5-32.8	11.73 ± 0.54 (25) 10.4-13.0	123.37 ± 3.80 (25) 115.5-132.0	228.53 ± 11.18 (22) 207.0-245.5
reconditus (E Pan-NW Col)	98.1 ± 1.6 (12) 88-123	M	35.79 ± 2.09 (28) 31.4-38.9	43.06 ± 2.67 (28) 38.3-47.2	29.14 ± 1.74 (28) 25.4-32.2	11.82 ± 0.40 (28) 10.8-12.7	127.96 ± 3.06 (27) 123.5-131.1	232.39 ± 11.13 (24) 209.0-256.5
		F	35.18 ± 2.06 (21) 31.4-37.8	41.89 ± 2.02 (21) 38.5-45.4	28.78 ± 2.12 (21) 25.9-35.5	11.72 ± 0.39 (22) 10.7-12.4	126.82 ± 2.82 (21) 123.0-132.6	230.61 ± 9.82 (18) 211.0-245.5
subrufescens (N + C Colombia)	96.0 ± 12.6 (27) 75-124	M	35.82 ± 1.70 (35) 33.4-39.4	42.05 ± 2.02 (35) 39.2-45.4	28.67 ± 1.70 (35) 24.5-32.8	11.33 ± 0.40 (35) 10.4-12.2	125.89 ± 3.06 (33) 118.5-131.6	226.20 ± 9.75 (30) 202.5-247.5
		F	34.33 ± 1.65 (32) 31.0-37.8	41.18 ± 2.17 (32) 35.5-45.4	27.61 ± 1.46 (32) 23.8-30.5	11.16 ± 0.55 (33) 10.0-12.4	123.86 ± 3.86 (33) 115.8-131.1	224.62 ± 7.86 (29) 209.5-239.0
osgoodi (NE Col-NW Ven)	94.8 ± 5.4 (7) 80-103	M	35.86 ± 1.02 (7) 33.7-37.9	42.21 ± 1.67 (7) 40.5-45.3	29.93 ± 1.10 (7) 27.8-30.7	11.67 ± 0.76 (7) 10.6-12.5	126.79 ± 2.77 (7) 122.3-130.4	227.50 ± 7.89 (6) 217.0-240.0
		F	34.93 ± 1.12 (8) 33.3-37.0	41.60 ± 1.66 (8) 39.3-44.3	27.96 ± 0.78 (8) 26.7-29.1	11.34 ± 0.51 (8) 10.7-12.3	123.98 ± 3.98 (8) 118.1-131.7	223.93 ± 14.95 (6) 203.5-247.0

Continuation Appendix 11. Means (± 1 standard deviation) and ranges of measurements of *Momotus* taxa from northern South America and southern Central America. All linear measurements in mm; sample sizes in parentheses. Data for sexes presented separately except for body mass (g).

Taxon	Body Mass (g)	Sexo	Measurements (mm)					
			Exposed Culmen	Total Culmen	Bill from Nostril	Bill depth at nostril	Closed Wing Chord	Tail length
Taxa and principal populations measured								
bahamensis (Trinidad-Tobago)	111.4 ± 13.1 (15) 89-133	M	37.53 ± 1.23 (12) 34.5- 39.0	44.33 ± 1.64 (12) 41.7-46.9	29.53 ± 0.75 (12) 27.8-30.8	12.18 ± 0.19 (12) 11.8-12.5	135.75 ± 2.19 (12) 132.3-139.2	223.58 ± 9.01 (10) 214.0-240.0
		F	37.16 ± 2.23 (8) 35.1-39.3	43.88 ± 2.62 (8) 40.6-47.4	29.48 ± 2.11 (8) 27.7-31.5	12.11 ± 0.70 (8) 11.7-12.8	133.49 ± 2.61 (8) 131.7-135.2	218.88 ± 10.52 (6) 215.5-235.0
argenticinctus (SW Ecuador)	96.8 ± 8.7 (5) 87-102	M	36.49 ± 2.93 (12) 32.4-40.8	42.77 ± 3.07 (12) 37.4-46.2	29.38 ± 2.63 (12) 26.3-34.6	11.43 ± 0.51 (12) 10.7-12.3	127.34 ± 4.30 (12) 122.3-134.6	226.64 ± 7.01 (10) 215.5-237.5
		F	36.07 ± 2.85 (12) 32.7-39.8	41.13 ± 2.58 (12) 37.9-44.1	27.72 ± 1.28 (12) 25.9-29.7	11.62 ± 0.59 (12) 10.8-12.4	124.53 ± 3.36 (11) 120.7-128.4	223.17 ± 13.29 (9) 213.0-238.5
microstephanus (E Colombia)	120.7 ± 14.0 (21) 95-153	M	36.28 ± 1.70 (65) 33.7-39.9	43.56 ± 1.86 (65) 39.7-47.2	29.54 ± 1.45 (65) 24.5-32.1	11.91 ± 0.52 (67) 10.2-12.8	133.33 ± 2.98 (66) 126.1-143.6	229.91 ± 10.52 (59) 202.0-256.5
		F	35.76 ± 1.85 (49) 30.4-39.5	43.15 ± 1.85 (49) 39.6-47.2	29.02 ± 1.68 (49) 24.3-32.0	11.82 ± 0.42 (51) 11.0-12.6	129.95 ± 3.54 (48) 123.3-138.6	224.19 ± 10.50 (44) 191.5-244.5
momota (S Venezuela)	144.4 ± 7.2 (5) 125-155	M	38.23 ± 2.46 (12) 35.3-42.4	46.47 ± 3.32 (12) 41.0-51.4	31.41 ± 1.87 (12) 29.5-34.5	12.92 ± 0.44 (12) 12.2-13.4	143.63 ± 3.29 (12) 139.0-150.3	260.92 ± 10.07 (11) 250.5-280.0
		F	36.39 ± 1.46 (10) 34.6-38.5	44.73 ± 1.50 (10) 42.0-46.5	29.87 ± 0.85 (10) 28.0-31.2	12.15 ± 0.52 (10) 11.5-13.0	140.99 ± 4.11 (10) 134.8-146.9	254.22 ± 8.87 (8) 242.0-268.5
aequatorialis (C,W Andes-Col)	163.5 ± 14.5 (23) 143-202	M	40.92 ± 1.74 (41) 36.4-45.1	48.91 ± 1.91 (42) 45.3-51.7	33.35 ± 1.60 (42) 28.3-36.3	13.37 ± 0.46 (44) 12.6-14.1	156.43 ± 4.58 (43) 146.5-167.5	298.40 ± 13.50 (39) 272.0-324.5
		F	40.54 ± 2.41 (32) 35.8-44.6	47.93 ± 2.19 32) 44.3-51.8	32.62 ± 1.98 (32) 28.4-36.5	13.16 ± 0.67 (33) 11.8-14.0	155.27 ± 5.73 (34) 144.9-168.0	288.68 ± 14.97 (30) 264.5-323.0
Other taxa and populations from peripheral areas								
spatha (N Colombia)		M	33.95 (2) 32.6-35.3	38.55 (2) 36.7-40.4	27.5 (2) 25.7-29.3	11.30 (2) 11.1-11.5	125.85 (2) 123.4-128.3	231.0 (2) 229.0-233.0

Continuation Appendix 11. Means (± 1 standard deviation) and ranges of measurements of *Momotus* taxa from northern South America and southern Central America. All linear measurements in mm; sample sizes in parentheses. Data for sexes presented separately except for body mass (g).

Taxon	Body Mass (g)	Sexo	Exposed Culmen	Total Culmen	Bill from Nostril	Bill depth at nostril	Closed Wing Chord	Tail length
Taxa and principal populations measured								
subrufescens (N Venezuela)		M	32.66 ± 0.98 (6) 31.6-34.3	40.74 ± 1.73 (6) 38.5-42.6	26.56 ± 0.66 (6) 25.9-28.6	10.99 ± 0.52 (6) 10.3-11.8	124.51 ± 1.67 (6) 122.0-126.3	231.00 ± 8.42 (6) 220.5-240.5
		F	32.04 ± 1.11 (6) 29.8-34.1	40.04 ± 1.31 (6) 36.2-43.0	26.67 ± 0.80 (6) 24.0-28.4	11.02 ± 0.44 (6) 10.6-11.7	123.77 ± 2.01 (6) 118.4-126.1	230.25 ± 10.11 (6) 215.0-241.5
microstephanus (Ecuador)		M	35.97 ± 0.81 (6) 34.5-36.8	43.50 ± 2.07 (6) 41.6-46.5	30.02 ± 1.12 (6) 28.3-31.2	11.93 ± 0.37 (6) 11.6-12.4	133.10 ± 2.04 (6) 129.9-136.0	226.83 ± 9.20 (5) 218.5-244.5
		F	34.88 ± 1.64 (6) 32.7-36.7	42.07 ± 1.96 (6) 39.8-44.5	28.23 ± 1.28 (6) 26.5-29.9	11.78 ± 0.48 (6) 11.1-12.5	128.02 ± 3.16 (6) 124.4-132.8	218.58 ± 10.34 (5) 207.5-237.5
aequatorialis (Ecuador)		M	40.55 ± 2.02 (5) 37.8-43.2	50.52 ± 1.28 (5) 48.7-51.7	33.82 ± 1.13 (5) 32.4-35.0	13.03 ± 0.74 (5) 12.4-14.0	157.05 ± 2.01 (5) 154.8-159.7	291.75 ± 13.20 (5) 279.0-305.5
		F	40.20 ± 2.87 (5) 36.3- 43.0	49.80 ± 1.29 (5) 48.2-50.9	33.40 ± 1.39 (5) 31.6-34.8	13.02 ± 0.66 (5) 12.1-13.5	156.70 ± 3.41 (5) 152.2-160.3	293.25 ± 13.87 (5) 276.5-309.0
chlorolaemus (Perú)		M	40.70 ± 1.74 (5) 38.8-42.5	50.58 ± 1.98 (5) 47.8-52.4	33.55 ± 1.39 (5) 33.0-35.6	13.45 ± 0.24 (5) 13.2-13.7	158.25 ± 1.85 (5) 156.5-160.0	296.50 ± 13.58 (5) 280.0-310.5
		F	40.40 ± 1.36 (5) 39.0-41.7	49.87 ± 0.78 (5) 49.0-50.5	33.63 ± 1.51 (5) 31.9-34.7	12.93 ± 0.51 (5) 12.5-13.5	156.33 ± 2.57 (5) 153.5-157.9	298.25 ± 7.42 (4) 293.0-303.5