ISSN 1794-0915

Ornitología Colombiana

PUBLICADO POR LA ASOCIACIÓN COLOMBIANA DE ORNITOLOGÍA

Número 8 - Junio 2009

ASOCIACION COLOMBIANA DE ORNITOLOGIA

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ORNITOLOGÍA COLOMBIANA

La Asociación Colombiana de Ornitología (ACO) inició actividades en 2002 con el fín de incentivar el estudio científico y la conservación de las aves de Colombia mediante la publicación de una revista, **Ornitología Colombiana**. La membresía en la Asociación está abierta a cualquier persona con interés por las aves colombianas y su conservación. Las cuotas para el 2009 son (dentro de Colombia, en pesos colombianos): $65.000 (profesionales), $50.000 (estudiantes con carné vigente), $1.625.000 (miembro benefactor o vitalicio). Se deben realizar las consignaciones en la cuenta de ahorros número 19113323615 de Bancolombia, a nombre de **Asociación Colombiana de Ornitología ACO**. Una vez realizado su pago, favor notificar por correo electrónico a secretario@ornitologiacolombiana.org dando el número de la consignación, la sucursal del banco y la fecha. Fuera de Colombia los pagos se realizan en dólares US: $40 (otros países latinoamericanos); $50 (otros países).

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UNIVERSIDAD NACIONAL DE COLOMBIA
SEDE BOGOTÁ
FACULTAD DE CIENCIAS
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Universidad de los Andes
Facultad de Ciencias

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Ornitología Colombiana No. 8, junio 2009

Artículos

Notas Breves

NOTA DE LOS EDITORES

En el editorial del número anterior de *Ornitología Colombiana* anunciamos que la revista había cumplido los requisitos para ser indexada a nivel internacional por Scopus (Elsevier) y nacionalmente por Publindex. La indexación en Scopus es ya un hecho: todos los artículos que hemos publicado están incluidos en esta amplia base de datos -lo que permite que sean encontrados por sus motores de búsqueda- e incluso ya existen vínculos que conducen a las publicaciones que los han citado. Sin duda, esto ha posicionado a *Ornitología Colombiana* de forma muy positiva a nivel internacional. También hemos logrado que la página web de la Neotropical Ornithological Society incluya un vínculo a la nuestra, otro incremento importante en la visibilidad de nuestra revista. Sin embargo, las noticias a nivel local son menos alentadoras, pues a última hora COLCIENCIAS conceptuó que la revista debía cumplir una serie de requisitos adicionales para poder ingresar formalmente a Publindex. Debido a que varios de ellos no se ajustan al tipo de publicación que representa *Ornitología Colombiana* (de libre acceso en internet, sin distribución masiva de copias físicas a suscriptores, etc.), estamos a la espera de concertar una cita con esa entidad para poder aclarar varios asuntos, lo que esperamos conduzca finalmente a la aparición de nuestra revista en su sistema de indexación.

Hablando del posicionamiento internacional que ha alcanzado *Ornitología Colombiana*, es notorio que cada vez recibimos más manuscritos presentando resultados de estudios realizados en países neotropicales distintos a Colombia. Prueba de ello son los artículos sobre el estudio de dietas de colibríes basado en análisis de isótopos estables de Jessica Hardesty y la descripción del nido de *Atlapetes latinuchus* hecha por Harold Greeney que publicamos en este número, ambos basados en datos obtenidos en Ecuador. Además, el análisis taxonómico del complejo de *Momotus momota* elaborado por Stiles abarca un ámbito geográfico bastante amplio, por lo que suponemos que llamará la atención de lectores de varios países de nuestra región. Nuestra política con respecto a la aceptación de estudios no realizados en Colombia es la de considerar para publicación aquellos manuscritos que pensamos que serían de interés para la mayor parte de nuestra audiencia, sea porque tratan aspectos de la biología de especies que también se encuentran en Colombia o porque abordan asuntos conceptuales o empíricos de interés, independientemente del ámbito geográfico. Así, conociendo que otros países del norte de Sur América y de América Central no cuentan con revistas ornitológicas con el perfil de la nuestra, estamos especialmente abiertos a recibir los trabajos de colegas de otros países.

En relación con el ámbito geográfico al que esperamos llegar con *Ornitología Colombiana*, vale la pena mencionar también nuestra política editorial con respecto a manuscritos basados en trabajos realizados a nivel local en Colombia. Nuestra meta es que todos los artículos publicados en la revista sean de interés para un rango amplio de lectores, no sólo en el ámbito nacional sino también en el internacional, por lo que sugerimos a todos los autores tener esto en mente al preparar sus contribuciones, particularmente aquellas que describen nuevos registros puntuales de especies para localidades del país. Los trabajos que presentan información nueva acerca de la distribución de las especies en Colombia son bienvenidos en la revista, como lo demuestra la publicación en este número de artículos que documentan el hallazgo de una nueva población de *Ognorhynchus icterotis* en la Cordillera Oriental (uno de los descubrimientos recientes de mayor interés para la ornitología de esta parte del continente, que representa una nueva oportunidad para la conservación de esta especie emblemática) y de nuevas localidades para *Cistothorus apolinari* y *Henicorhina negreti* (dos especies endémicas colombianas que se encuentran amenazadas y son poco conocidas). Sin embargo, en los últimos meses nos hemos abstenido de considerar algunos manuscritos que presentan información nueva sobre distribución de especies debido a que, pensando en nuestra audiencia, juzgamos que los registros no representaban extensiones demasiado significativas o inesperadas de las distribuciones conocidas como para ser de interés en el ámbito internacional. La información contenida en aquellos manuscritos bien podría publicarse, pero no nos parece que *Ornitología Colombiana* sea el foro más adecuado. Así, nos gustaría animar a aquellos autores que no han recibido una respuesta positiva de nosotros a que consideren publicar sus datos en otro medio. Por ejemplo, aunque cada vez se internacionaliza más, el Boletín de la Sociedad Antioqueña de Ornitología es un excelente foro para la publicación de información de interés en un contexto más local.

Finalmente, pedimos excusas a nuestros lectores por la tardanza en la publicación de este número de *Ornitología Colombiana*, que hemos terminado varias semanas más tarde de lo presupuestado. Parte de la demora se debió a cambios en la organización de la Asociación Colombiana de Ornitología. Desde hace unos meses estamos trabajando con Tatian Celeita como nueva coordinadora y Diego Soler (quien además actúa como Secretario de la Junta Directiva) se ha encargado de las tareas de diagramación de la revista. Con la experiencia adquirida por ellos en esta etapa, esperamos ser más ágiles en el futuro y seguimos con nuestra meta firme de publicar dos números anuales de la revista. Esperamos que quienes han esperado pacientemente por este número se sientan recompensados con la calidad y variedad de los artículos que contiene.

F. Gary Stiles & Carlos Daniel Cadena
Editores, *Ornitología Colombiana*

AGRADECIMIENTOS

Como siempre, estamos inmensamente agradecidos con los evaluadores que han contribuido con su tiempo y experticia para dar su concepto sobre los manuscritos presentados a *Ornitología Colombiana.* Para este número contamos con la valiosa colaboración de Humberto Álvarez-López, C. Daniel Cadena, Andrés M. Cuervo (dos manuscritos), Jeanne Fair, Keith A. Hobson, Fabián Jaksic, Manuel Marín, Ulyses Pardiñas, Luis Miguel Renjifo, Katherine Renton, Mark B. Robbins, Adriana Rodríguez-Ferraro, F. Gary Stiles y Christopher Witt. Dentro de la Asociación, agradecemos a Loreta Rosselli por su trabajo silencioso y minucioso en el mantenimiento de nuestra página web, incluyendo el montaje de *Ornitología Colombiana.* Con la coordinación eficiente de Tatian Celeita y la diagramación de Diego Soler, confiamos en que el trabajo de edición de la revista será más ágil de aquí en adelante.

Nuestra portada: Un adulto de *Momotus a. aequatorialis,* el miembro más grande del género. Esta forma antes se consideraba una subespecie de *Momotus momota*; véase el artículo de F.G. Stiles (págs. 29-75). Foto tomada por Juan David Ramírez en Medellín, Antioquia, cerca de El Poblado.

Artículos

CRECIMIENTO Y DESARROLLO DEL PLUMAJE EN PICHONES DE LA COTORRA ALIAZUL (*HAPALOPSITTACA FUERTESI*) EN LA CORDILLERA CENTRAL COLOMBIANA

Growth and plumage development of Azure-winged Parrot (*Hapalopsittaca fuertesi*) nestlings in the Central Andes of Colombia

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RESUMEN

La Cotorra Aliazul (*Hapalopsittaca fuertesi*) es una especie endémica de Colombia que se encuentra en peligro crítico de extinción y existe poca información sobre su biología que permita contribuir a su conservación. En este trabajo presento datos sobre el crecimiento de 25 pichones de *H. fuertesi* obtenidos entre enero y julio de 2005 en un área de bosque altoandino del departamento del Quindío. Describí los patrones de crecimiento en la masa, la longitud de las plumas primarias, la longitud del pico y la longitud de la cola utilizando una ecuación logística, y comparé mis datos con los obtenidos para otras especies de psitácidos. Además, describí la secuencia en que aparecen las plumas verdaderas en la cabeza, el cuerpo, las alas y la cola, a lo largo de la permanencia de los pichones en el nido (58.8 días en promedio). La masa alcanzó un valor asintótico durante una fase temprana del período de cría de los pichones, al igual que algunos psitácidos neotropicales de talla similar. Sin embargo, la tasa de crecimiento observada en *H. fuertesi* fue más similar a la de especies de psitácidos de tierras bajas de mayor talla, lo que podría deberse a una disponibilidad de alimento reducida en zonas altoandinas. Las curvas de crecimiento obtenidas para las medidas corporales, junto con los patrones de aparición del plumaje descritos en este trabajo, son herramientas útiles para estimar la edad de pichones de edad desconocida y podrían ser de utilidad para programas de cría en cautiverio.

Palabras clave: Colombia, desarrollo del plumaje, *Hapalopsittaca fuertesi,* pichones, tasas de crecimiento.

ABSTRACT

The Azure-winged Parrot (*Hapalopsittaca fuertesi*) is an endemic and critically endangered species from Colombia for which biological information that might aid conservation efforts is largely lacking. In this study, I present data on growth of 25 nestlings of *H. fuertesi* obtained in January-July 2005 in a high Andean forest area in depto. Quindío. I described growth in body mass, primary feather length, bill length and tail length using a logistic equation, and compared my data with those available for other species of psittacids. In addition, I described the sequence in which true feathers appear on the head, body, wings, and tail during the permanence of chicks in the nest (average 58.8 days). Body mass reached an asymptotic value during an early phase of the nestling period, as in other psittacids of similar size. However, the growth rate observed in *H. fuertesi* was more similar to that of lowland species of psittacids of larger size, which might be due to reduced food availability in high Andean areas. The growth curves obtained for body measurements, together with patterns of plumage development described in this study, are useful tools to estimate the age of nestlings of unknown age and can be useful for captive breeding programs.

Key words: chicks, Colombia, growth rate, *Hapalopsittaca fuertesi*, plumage development.

INTRODUCCIÓN

El riesgo de extinción al que se enfrentan actualmente los psitácidos es alarmante: el 24% de las 356 especies de loros del mundo se encuentran en riesgo y el 10% (36 especies) están cercanas a la extinción (Collar 1996, Snyder *et al.* 1992). La situación es especialmente grave en el Neotrópico, una región que alberga el 40% (140) de las especies de loros del mundo, de las cuales el 31% (44) se encuentran en riesgo de extinción (Collar 1996). Dentro del Neotrópico, la región andina sobresale como prioritaria para la conservación pues alberga a un grupo heterogéneo de loros amenazados que incluye especies de siete géneros (Collar 1996). Específicamente, en los Andes de Colombia se encuentran ocho especies amenazadas de loros andinos, de las cuales cuatro son endémicas del país.

Entre las principales amenazas que pesan sobre los loros andinos están la pérdida de su hábitat y el tráfico ilegal debido a su alta demanda como mascotas (Collar & Juniper 1992). Además, su naturaleza monógama y su fidelidad a los sitios de anidación los hace un grupo particularmente frágil ante perturbaciones de sus actividades reproductivas (Masello & Quillfeldt 2002). Aunque existe un creciente interés por la conservación de los psitácidos, aún existen grandes vacíos en cuanto a información básica sobre la biología de muchas de las especies más amenazadas (Snyder *et al.* 1992, Collar 1996, Renjifo *et al.* 2000). Estos vacíos impiden la planeación de estrategias de conservación efectivas (Collar 1996).

La Cotorra Aliazul (*Hapalopsittaca fuertesi*) es una especie endémica de Colombia que se encuentra en peligro crítico de extinción (CR) debido al deterioro de su hábitat natural y a la consecuente reducción de su área de distribución (Renjifo 2002). Actualmente, se cree que la especie se encuentra limitada a los bosques altoandinos de la Cordillera Central ubicados en algunos municipios del sur de Caldas, el oriente de Risaralda, el nororiente del Quindío y el occidente del Tolima (Renjifo 2002). Esta distribución pequeña hace que la especie sea particularmente vulnerable, especialmente si se tiene en cuenta su distribución altitudinal estrecha (2600–3500 m; Renjifo 2002).

Tras ser descrita por Chapman (1912), la Cotorra Aliazul se creyó extinta hasta finales de la década de l980, cuando se empezaron a registrar algunas observaciones (Stattersfield & Capper 2000, Renjifo 2002). Sin embargo, el seguimiento constante a poblaciones de esta especie se inició sólo en 2003 con el establecimiento de la Reserva Municipal Natural "El Mirador" por parte de la Fundación ProAves-Colombia en el municipio de Génova, Quindío. Allí se han realizado esfuerzos por acrecentar el conocimiento acerca de la especie y por contribuir con su conservación. Por ejemplo, en 2003, ProAves instaló 120 nidos artificiales en esta reserva y en dos fincas aledañas con el fin de disminuir la competencia por las escasas cavidades naturales existentes entre las especies de psitácidos del área (Quevedo *et al.* 2006). Los nidos artificiales fueron ocupados exitosamente de forma inmediata por parte de la Cotorra Aliazul y del Perico Paramuno (*Leptopsittaca branickii*), lo que permitió iniciar estudios como el de Quevedo *et al.* (2006) sobre algunos aspectos ecológicos y reproductivos y el de Tovar-Martínez (2006) sobre la biología reproductiva de *H. fuertesi*. Estos estudios indicaron que la Cotorra Aliazul habita en bosques altoandinos amplios, maduros y con niveles medios de intervención por ganadería (Quevedo *et al.* 2006). La especie es difícil de detectar debido a que vuela a ras de dosel y emite vocalizaciones poco ruidosas, y a la permanente presencia de niebla en su hábitat (Tovar-Martínez, datos no publicados). Además, la especie parece no realizar movimientos amplios en busca de sitios de alimentación y se desplaza generalmente en grupos de 7-15 individuos, frecuentemente en busca de frutos de la hemiparásita *Antidaphne viscoidea* (Eremolepidaceae; Quevedo *et al.* 2006). La reproducción de la Cotorra Aliazul tiene lugar durante el primer semestre del año, lo que coincide con la reproducción de la Cotorra Montañera (*H. amazonina velezi*) en la región (Quevedo *et al.* 2006, Tovar-Martínez 2006), pero contrasta con un informe acerca de la reproducción de la Cotorra Carirroja (*H. pyrrhops*) durante el segundo semestre del año en Ecuador (Toyne & Flanagan 1996).

Aunque Quevedo *et al.* (2006) tomaron medidas morfométricas de pichones de la Cotorra Aliazul, de la Cotorra Montañera, del Perico Paramuno y del Loro Orejiamarillo (*Ognorhynchus icterotis*), el desarrollo de éstos no ha sido evaluado en detalle en ninguno de los loros andinos amenazados, a pesar de la importancia que este tipo de información puede tener para el estudio y la conservación de las especies amenazadas (Saunders 1986). Por ejemplo, conocer los patrones naturales de crecimiento de los pichones tendría aplicaciones como la de poder determinar la edad de aves jóvenes encontradas en el campo, y desde una perspectiva más aplicada, este tipo de información sería de utilidad para el manejo de aves en cautiverio (Navarro & Bucher 1990). Además, los vacíos de información impiden hacer comparaciones entre estas especies de loros y otras mejor estudiadas en términos de parámetros relacionados con sus historias de vida. Específicamente, hasta el momento no existen estimaciones de la tasa de crecimiento de los pichones de especies de loros andinos, lo que impide realizar análisis comparativos con respecto a especies neotropicales de tierras bajas (Navarro & Bucher 1990, Aramburú 1997, Masello & Quillfeldt 2002, Renton 2002) o de otras regiones (ej. Australia, ver Saunders 1982, Krebs 1999). Enfocándome en datos obtenidos para la Cotorra Aliazul en 2005, en este trabajo presento los primeros análisis del crecimiento y desarrollo del plumaje en una especie andina de loro, y establezco comparaciones con datos similares obtenidos para especies de loros neotropicales de tierras cálidas.

MATERIALES Y MÉTODOS

Realicé este trabajo en tres localidades ubicadas entre los 3000 y 3500 m de elevación en las veredas Pedregales y Río Gris, municipio de Génova, Quindío, en el flanco occidental de la Cordillera Central colombiana (Fig. 1). Las tres

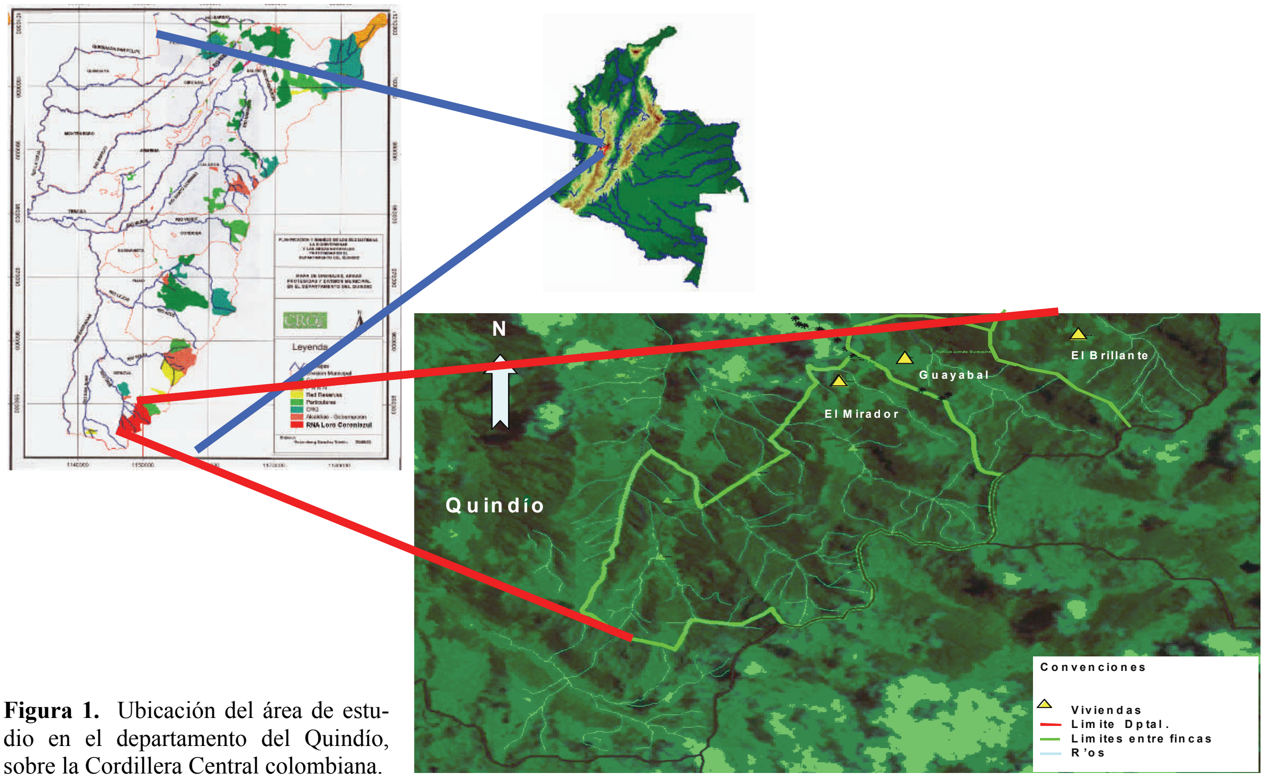

Figura 1. Ubicación del área de estudio en el departamento del Quindío, sobre la Cordillera Central colombiana.

localidades son la Reserva Municipal Natural El Mirador (4º08’ N, 75º44' W), la Finca Guayabal (4º09' N, 75º44’ W) y la Finca Brillante (4°09' N, 75°43' W), que forman un corredor en donde es frecuente observar la Cotorra Aliazul. Los bosques altoandinos del área poseen troncos retorcidos, con hojas pequeñas y coriáceas, y están densamente poblados de plantas epífitas que tapizan los árboles y les dan una alta variedad de tonos y formas (Cuatrecasas 1958, Brown & Kappelle 2001, Gentry 2001). Algunos de los géneros de árboles y arbustos más representativos son *Weinmannia*, *Ilex*, *Escallonia*, *Miconia* y *Hesperomeles* (Rodríguez *et al.* 2004, Carantón 2005). Rangel (2000) señala que en la Cordillera Central existe un régimen de distribución de lluvias de tipo bimodal-tetraestacional, con una precipitación total anual aproximada de 1850 mm y una temperatura de 6 a 12ºC para la elevación a la que realicé este estudio.

De enero a julio de 2005 monitoreé los nidos artificiales y naturales de la Cotorra Aliazul que se encontraban activos en el área de estudio. Para la detección de actividad en los nidos realicé una caminata quincenal durante los dos primeros meses a lo largo de tres senderos, alrededor de los cuales se habían instalado nidos artificiales o existían potenciales nidos naturales previamente identificados. Durante estas caminatas, inspeccioné el interior de las cavidades subiendo a los árboles o con ayuda de una escalera. Tambien busqué nidos activos observando aves que volaban por encima del dosel desde puntos de observación con un margen de visión de aproximadamente 120° (Ralph *et al.* 1996), los cuales estuvieron ubicados aproximadamente cada 150m a lo largo de los tres senderos. Realicé observaciones durante dos días por cada sendero, completando entre siete y nueve puntos de observación diariamente entre las 6:00 y las 18:00h. En cada punto esperé por un espacio de tres horas, y estuve alerta a observar comportamientos de individuos adultos y jóvenes que pudieran indicar la ocupación de un nido (Ralph *et al.* 1996).

Debido a que las hembras permanecían en los nidos la mayor parte del tiempo durante las primeras semanas de la anidación, no fue posible inspeccionar con detalle los nidos con huevos y con crías de menos de dos semanas de edad. Por lo tanto, durante estas etapas sólo evalué la fecha de eclosión, el desarrollo de las crías a nivel general y algunos caracteres físicos como su coloración, la presencia de plumón y la aparición de plumas verdaderas. A partir de la tercera semana después de la eclosión, cuando las hembras comenzaron a dejar sus nidos temporalmente para unirse a los machos en la búsqueda de alimento, inicié monitoreos detallados en los que examiné cada nido semanalmente hasta que las crías lo abandonaron. Los monitoreos incluyeron la realización de observaciones sobre la aparición y el desarrollo del plumaje, y el registro de medidas morfométricas para establecer patrones de crecimento. Para diferenciar a cada uno de los pichones, los marqué con anillos de aluminio numerados que fueron ubicados en el tarso derecho durante la tercera o cuarta semana de desarrollo.

Durante las observaciones semanales sobre el desarrollo del plumaje, registré información acerca de la aparición de plumas verdaderas separadamente para la cabeza, el cuerpo, la cola y las alas de los pichones. Para esto, realicé anotaciones generales acerca de las zonas en donde aparecieron los primeros cañones y describí su desarrollo a través del tiempo en términos del tamaño y coloración de las plumas. Además, registré caracteres adicionales como el color del pico y de los ojos.

Para cada uno de los pichones, tomé cuatro medidas corporales semanalmente, siguiendo las recomendaciones de Baldwin *et al.* (1931), Ralph *et al.* (1996) y Enkerlin-Hoeflich *et al.* (1998): la longitud del culmen expuesto sin cera (medida en línea recta desde el extremo de la maxila hasta el borde anterior de la cera), la longitud de las primarias (desde el extremo hasta el lugar de inserción), la longitud de la cola (desde el extremo hasta el lugar de inserción de las retrices centrales) y el peso. Las medidas de longitud fueron tomadas con un calibrador “SPI 2000” con una precisión de 0.1 mm y la masa con balanzas de 60 y 600 g. Examiné en total 25 pichones (ver Resultados), pero debido a imprevistos (e.g. abandono del nido, dificultades climáticas), en algunas ocasiones tuve muestras menores.

Para describir el desarrollo de los pichones por medio de curvas de crecimiento, calculé el promedio diario de cada medida corporal usando los datos de todos los individuos, sin hacer distinciones entre los nidos y sin considerar el orden de nacimiento. La asincronía en el nacimiento generó que la muestra variara diariamente: en algunos días no pude obtener mediciones para ningún polluelo y en otros obtuve datos hasta para cuatro individuos. Las curvas de crecimiento fueron construidas usando el programa CurveExpert versión 1.3 para Windows (Hyams 1993), especificando la ecuación logística de Ricklefs (1967) como modelo de regresión no lineal. Seleccioné esta ecuación (ver también Salinas-Melgoza 1999, Renton 2002) porque presentó un mejor ajuste a mis datos de acuerdo al coeficiente de determinación (R^2) que las ecuaciones de Gompertz y von Bertalanffy (ver detalles en Ricklefs 1967).

RESULTADOS

El huevo de *H. fuertesi* es de coloración blanca, con forma esférico-elíptica y unas dimensiones de 35.6 x 28.5 mm (n=1). Fue posible obtener información detallada sobre el desarrollo y crecimiento para los 25 pichones que salieron de los nidos exitosamente durante la temporada; éstos procedían de 10 de los 12 nidos activos que monitoreé, en donde se criaron entre uno y tres individuos por nido (Tovar-Martínez 2006). En promedio (± desviación estándar), los pichones pasaron 58.81±2.45 días en el nido desde el momento de la eclosión hasta que lo abandonaron (ámbito 55-64.5 días; n=22; para tres pichones no obtuve datos suficientes para determinar su fecha exacta de eclosión o salida del nido).

DESARROLLO DEL PLUMAJE.- Al momento del nacimiento, las crías tenían los párpados fusionados, cubriendo el globo ocular de color negro. La piel tenía una coloración rosada a roja y estaba cubierta por un plumón blanco, liso y esponjado (Fig. 2). A partir de la segunda semana, los polluelos empezaron a abrir los ojos y progresivamente fue apareciendo un nuevo plumón tupido y grisáceo con igual tonalidad en todo el cuerpo que reemplazó el primero. En este período los polluelos se hicieron más fuertes, siendo capaces de levantar la cabeza por sí mismos. Al finalizar la segunda semana, empezaron a aparecer los primeros cañones de la cabeza y el ala en algunos de los individuos (Fig. 2).

En la tercera semana, los ojos de los pichones estaban completamente abiertos y los cañones de las plumas de la cabeza emergieron en la frente. Además, salieron las primeras plumas en el área de la mejilla, el área auricular y la parte superciliar de cada ojo (Fig. 2). En la mayor parte de los individuos (83.3%), aparecieron también los cañones de las plumas primarias y de las coberteras de las primarias, y uno o dos cañones de las plumas secundarias y las coberteras menores. Todas las plumas emergentes fueron de color amarillo verdoso. Al comenzar la cuarta semana, las plumas del álula y algunas coberteras menores mostraron su característico color rojizo; las plumas primarias, secundarias y coberteras de las primarias mostraron un color negro con algunos visos azules. En todos los individuos, los cañones faltantes de las plumas de las alas, de las caudales, de las infracaudales y de las supracaudales aparecieron a lo largo de esta semana. Los primeros cañones del cuerpo aparecieron en las tibias y el pecho de los individuos. Un pichón de aproximadamente cuatro semanas de crecimiento fue disectado, y se determinó que poseía un patrón de osificación de línea media (Pyle 1997), describiendo dos amplias ventanas de borde rojo; el porcentaje de osificación era aproximadamente de un 20%.

Para la quinta semana, los cañones que emergieron inicialmente en las tibias y el pecho fueron extendiéndose gradualmente hasta el vientre, y las plumas del resto del cuerpo continuaron su desarrollo, empezando a evidenciar los colores característicos de la especie (Fig. 2). La muda del plumón de la cabeza fue rápida y desde la sexta semana, algunos individuos (11.1%) lo habían reemplazado completamente por plumas verdaderas. También en la sexta semana, aparecieron plumas en el dorso que se extendieron lentamente hasta el límite con la rabadilla. Para la séptima semana, el plumón de la cabeza, las alas y la cola de los individuos había desaparecido casi por completo. El dorso se mostró progresivamente más cubierto por plumaje.

La octava semana fue típicamente la última de

Figura 2. Desarrollo de pichones de la Cotorra Aliazul y contraste con un adulto capturado: **a**. primera semana, **b.** segunda semana, **c**. tercera semana, **d**. quinta semana, **e.** y **f.** juvenil previo al primer vuelo (octava semana), **g.** y **h.** hembra adulta.

permanencia de los pichones en el nido. Para este momento, las plumas primarias y las coberteras de las primarias eran dorsalmente negras, con visos de color azul rey. Las plumas secundarias también eran negras, pero presentaban visos verdes. En la cara ventral de todas las plumas del ala se evidenció un color azul aguamarina similar al de las plumas caudales. Las primarias conservaron aproximadamente 1cm de cáñamo en su base, días antes del vuelo. La corona azul típica de la especie fue levemente visible. Las plumas caudales presentaron un color vinotinto en la base y azul rey desde la mitad de la pluma hasta el extremo en la parte dorsal; en la parte ventral, se hizo completamente distinguible el color azul aguamarina que es típico de la especie. Las plumas caudales conservaron parte del cañón durante la última semana de desarrollo. El color del cuerpo de los pichones en esta semana era en general verde claro, aunque un poco más opaco en la parte dorsal. Algunas plumas del centro del abdomen presentaban manchas anaranjadas aisladas, como en los adultos. Ningún individuo había mudado completamente el plumón del cuerpo hasta esa etapa, pues la rabadilla, los flancos y el pecho conservaron algo de plumón hasta la salida del nido. El pico de los polluelos presentó una coloración oscura durante su estadía en el nido: la maxila era negra desde la base hasta dos tercios de su extensión, y sólo el tercio restante era claro como en los adultos. La mandíbula tenía las mismas tonalidades pero sólo el tercio más proximal era de color negro. Otra diferencia notoria con los adultos fue la presencia de un anillo periocular blanquecino en los juveniles, mientras que los adultos muestran un anillo oscuro (Fig. 2).

CRECIMIENTO.- De acuerdo con la curva de crecimiento logística construida con datos tomados a partir de la tercera semana de vida, la longitud del pico de una cría de *H. fuertesi* recién nacida sería de 6.5 mm (Fig. 3). A partir de ese tamaño, el pico crece hasta alcanzar los 8.2 mm en el día 10, cuando la tasa de crecimiento es máxima (Tabla 1)

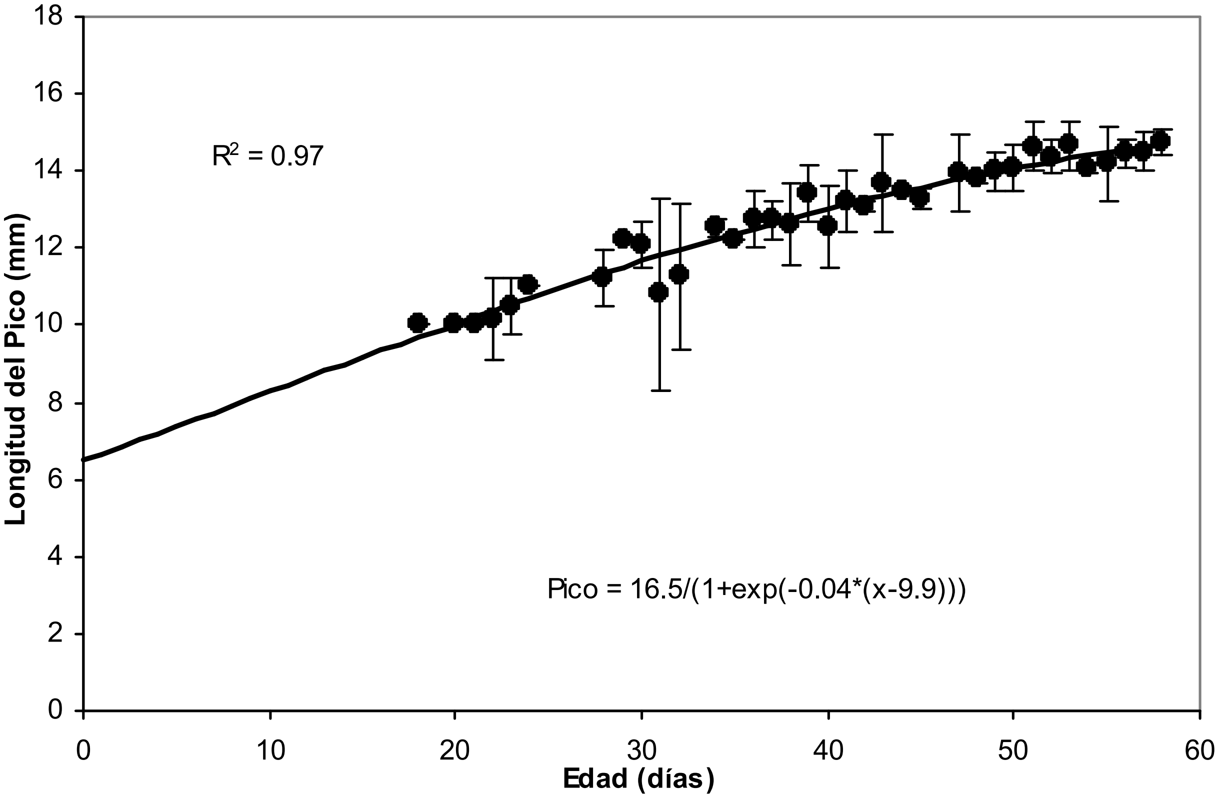

Figura 3. Crecimiento del pico de 25 pichones de Cotorra Aliazul en la Cordillera Central colombiana. La línea representa los valores esperados según la ecuación logística de Ricklefs (1967) y los puntos son los valores promedio observados. Las barras de error representan la desviación estándar.

Tabla 1. Parámetros de crecimiento en cinco medidas estimados para pichones de la Cotorra Aliazul a partir de la ecuación logística de Ricklefs (1967).

Variable	Numero de mediciones	Asíntota (A)	Tasa de crecimiento (K)	Punto de inflexión (t_i)	Ajuste de la curva (r^2)
Longitud del Pico (mm)	123	16.505	0.0437	9.904	0.974
Longitud de la Cola (mm)	121	91.722	0.101	39.490	0.989
Longitud de las Primarias (mm)	110	125.375	0.108	36.912	0.992
Masa (g)	120	129.352	0.132	15.535	0.962

y llega a una longitud promedio de 14.50±0.56 mm (ámbito 13.1-15.7 mm, n=21) en la semana previa al primer vuelo. Esta longitud corresponde al 86% de la medida en dos individuos adultos capturados (16.85±1.1 mm).

El crecimiento del plumaje se inició en una etapa tardía del desarrollo de las crías, pero la curva logística asigna valores para ambas variables desde el nacimiento, cuando aún no han aparecido los primeros cañones (Fig. 4 y 5). Durante la semana previa al primer vuelo, la cola de los juveniles alcanzó una longitud promedio de 76.04±7.43 mm (ámbito 60.4-89.0 mm, n=19) y las plumas primarias una longitud promedio de 110.2±7.7 mm (ámbito 96.4-120.8 mm, n=20). Estos datos equivalen al 76.6% de la longitud de la cola (99.2±5.4mm) y al 88.1% de la longitud de las primarias (125.5±18.2 mm) de los dos adultos medidos.

Al nacer, los polluelos pesarían aproximadamente 16.5g de acuerdo a la extrapolación basada en la curva de crecimiento (Fig. 6). Esta masa inicial se

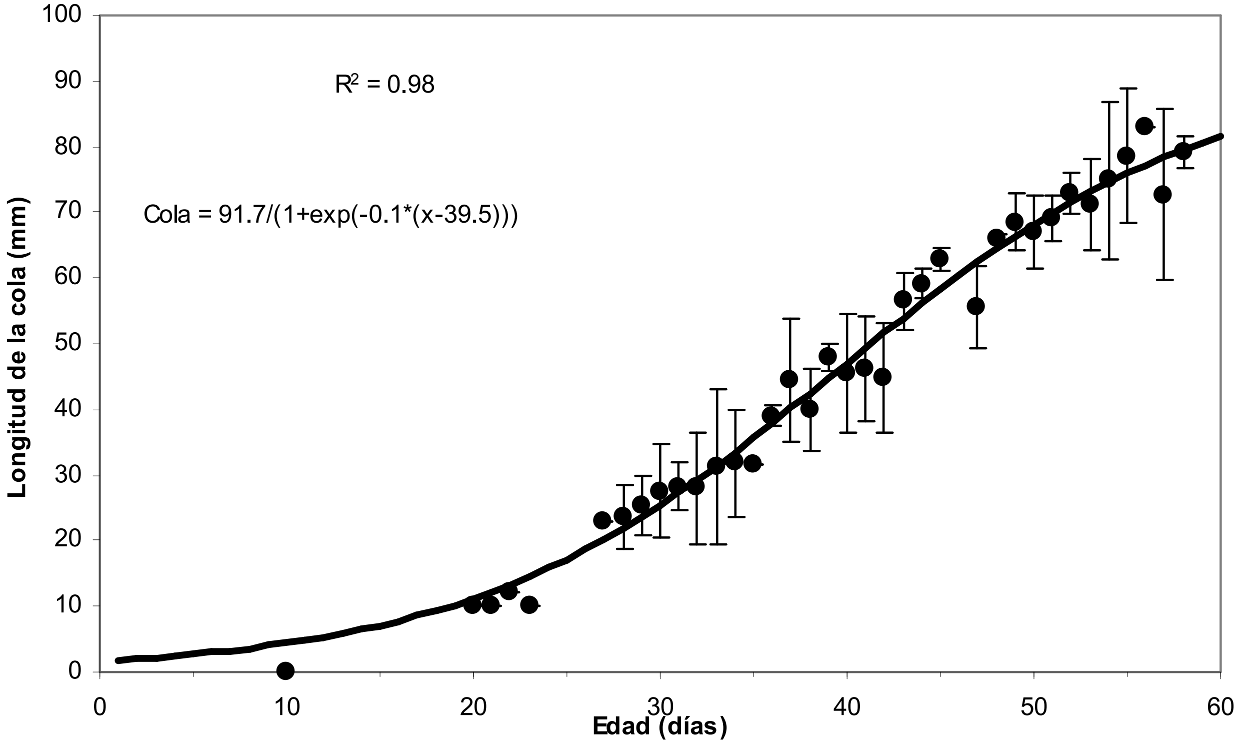

Figura 4. Crecimiento de la cola de 25 pichones de Cotorra Aliazul en la Cordillera Central colombiana. La línea representa los valores esperados según la ecuación logística de Ricklefs (1967) y los puntos son los valores promedio observados. Las barras de error representan la desviación estándar.

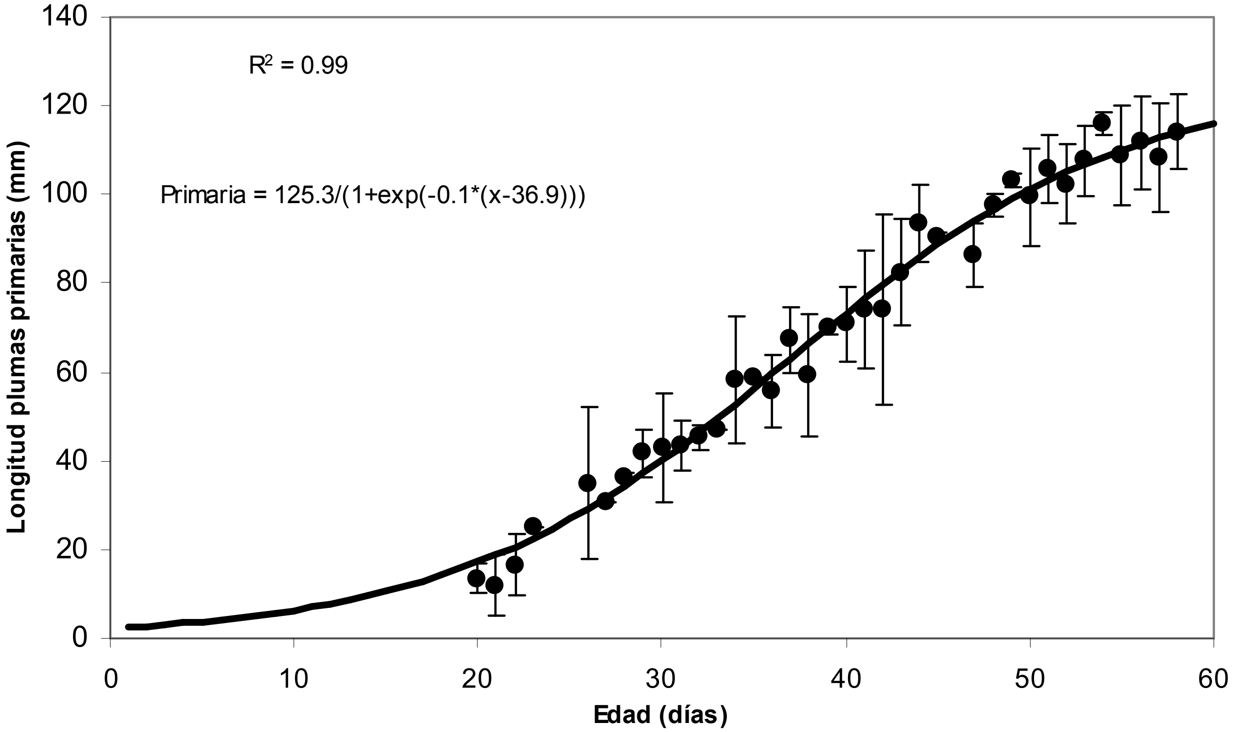

Figura 5. Crecimiento de las plumas primarias de 25 pichones de Cotorra Aliazul en la Cordillera Central colombiana. La línea representa los valores esperados según la ecuación logística de Ricklefs (1967) y los puntos son los valores promedio observados. Las barras de error representan la desviación estándar.

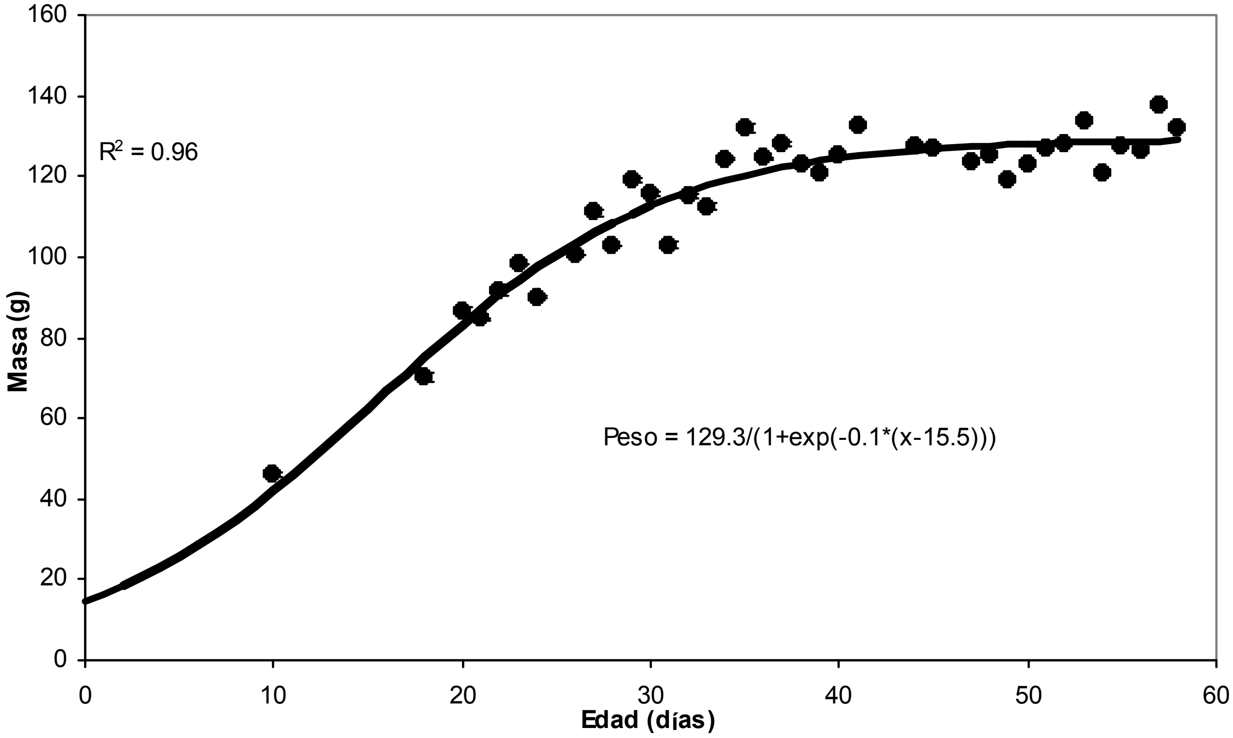

Figura 6. Desarrollo de la masa de 25 pichones de Cotorra Aliazul en la Cordillera Central colombiana. La línea representa los valores esperados según la ecuación logística de Ricklefs (1967) y los puntos son los valores promedio observados. Las barras de error representan la desviación estándar. La primera medición corresponde a la reportada por Quevedo *et al.* (2006).

incrementó progresivamente hasta alcanzar un peso máximo de 135.3 g ± 7.2 (ámbito: 125-148 g, n= 24) a los 44.5±7.6 días (ámbito 32-57 días, n=25). La masa máxima promedio es 11.3g superior a la masa de los adultos (124±12.7 g, n=2). Sin embargo, el 70.9% de los individuos mostraron una pérdida de masa en los 5 a 15 días anteriores a su salida del nido correspondiente a cerca del 9% con respecto a la masa promedio máxima obtenida (Fig. 6). Debido a esto, en la etapa inicial del desarrollo la tasa de crecimiento en masa fue mayor que la estimada para otras variables, lo que permitió que la masa alcanzara su valor máximo en una etapa comparativamente temprana del desarrollo.

DISCUSIÓN

Este estudio describe por primera vez el desarrollo del plumaje y el crecimiento de los pichones de la Cotorra Aliazul, una especie de psitácido de la cordillera de los Andes. En comparación con la información existente sobre el desarrollo de los pichones de otras especies de loros, dos patrones son especialmente notables. Primero, los pichones de la Cotorra Aliazul presentan una tasa de crecimiento más baja que la esperada para una especie de su tamaño (Tabla 2). Por ejemplo, con una masa asintótica de 129 g, la Cotorra Aliazul es sólo ligeramente más grande que *Myiopsitta monachus monachus*, una especie en la que la tasa de crecimiento de los pichones es de 0.248 (Aramburú 1997). En contraste, la Cotorra Aliazul presenta una tasa de crecimiento de 0.132, que es más similar a la especies de tamaño corporal mucho mayor, como *Amazona finschi* (325.7 g, Salinas-Melgoza 1999) e incluso *Ara macao* (1135g, datos no publicados mencionados por Renton (2002)). Segundo, los polluelos de la Cotorra Aliazul pasan un período de tiempo en el nido (58.8 días) bastante más largo que los polluelos de otras especies de loros de talla similar (e.g. 40 días en *Myiopsitta monachus*, Aramburú 1997; Tabla 2). Nuevamente, mis observaciones sobre la Cotorra Aliazul son más similares a las hechas en loros de mayor tamaño: los pichones de *Prosopeia tabuensis* (277g) abandonan el nido a las siete semanas (Rinke 1989) y los de algunas especies de *Amazona* (e.g. *A. finschi*, 325.7 g) lo hacen a las ocho o nueve semanas (Salinas-Melgoza 1999).

Ricklefs (1968b) señaló que la tasa de crecimiento y el tiempo que pasan los polluelos en el nido están fuertemente relacionados ya que las especies en las que los pichones pasan más tiempo en el nido pueden tener tasas de crecimiento más lentas y la carga alimenticia que los padres entregan a sus polluelos es relativamente baja. En cambio, los polluelos de especies con tasas de crecimiento mayores y un menor tiempo de permanencia en el nido requerirían de un mayor aprovisionamiento de alimento por parte de los padres. Por lo tanto, se esperaría que las tasas de crecimiento fueran mayores y los tiempos de permanencia en el nido menores en especies para las que la disponibilidad de alimento no es limitante. De hecho, Navarro & Bucher (1990) sugirieron que las tasas de crecimiento de los pichones de psitácidos se ven afectadas por factores ambientales, y Renton (2002) demostró que las variaciones en la disponibilidad

Tabla 2. Comparación de la asíntota y constante de crecimiento (k) de la masa entre varias especies de psitácidos.

Especie	Asíntota de Masa (g)	Constante (k)	Fuente
Anodorhynchus hyacinthinus	1500	0.11	Abramson (1991)
Ara macao	1135	0.139	Renton (2002)
Prosopeia tabuensis	277	0.162	Rinke (1989)
Cacatua pastinator pastinator	275	0.23	Smith (1991)
Forpus passerinus	23.7	0.23	Waltman & Beissinger (1992)
Amazona finschi	325.7	0.148	Salinas-Melgoza (1999)
Myiopsitta monachus catita	103.9	0.24	Navarro & Bucher (1992)
Myiopsitta m. monachus	106	0.248	Aramburú (1997)
Hapalopsittaca fuertesi	129.35	0.132	Este estudio

de alimento afectan la tasa de crecimiento de los pichones de *Amazona finschi*, los cuales crecen más rápidamente en años en los que la disponibilidad de alimento es mayor como consecuencia de aumentos en las lluvias. En conjunto, estas ideas sugieren que la tasa lenta de crecimiento y el tiempo comparativamente largo que pasan los pichones de la Cotorra Aliazul en los nidos podrían estar relacionados con una disponibilidad de alimento relativamente baja para esta especie, lo que es probable considerando que ésta habita ambientes fríos por encima de los 3000 m, en los que las fuentes de alimento podrían ser limitadas o inestables (ver Fjeldså 2001). Para probar esta hipótesis, sería necesario realizar un seguimiento fenológico anual a las especies de plantas de las que se alimenta la Cotorra Aliazul y evaluar si en años con condiciones más favorables se presenta un crecimiento más rápido de los pichones. De modo más general, mis resultados sugieren que podrían existir diferencias en el crecimiento de los pichones entre especies de loros de tierras altas y de tierras bajas, posiblemente como resultado de diferencias en la disponibilidad de alimento. Sin embargo, realizar más estudios sobre la reproducción de especies de loros de tierras altas es de vital importancia para evaluar la generalidad del patrón sugerido por este estudio. Además, para poner a prueba esta hipótesis, es necesario realizar estudios que cuantifiquen las diferencias en la disponibilidad de alimento para loros entre tierras bajas y tierras altas.

Mis observaciones indican que los pichones de la Cotorra Aliazul presentan dos plumones previos a las plumas verdaderas (blanco y gris), al igual que los pichones de *Myiopsitta m. monachus* (Aramburú 1997). Sin embargo, en la Cotorra Aliazul el plumón gris es bastante esponjado y cubre completamente la piel de los polluelos, a diferencia de lo observado en polluelos de especies de psitácidos de tierras bajas, cuyos plumones son ligeros y cuya piel es parcialmente visible hasta que empiezan a aparecer las plumas verdaderas (Lanning & Shiflett 1983, Renton 2002). Esto quizás esté relacionado con la necesidad de más aislamiento térmico en ambientes más fríos, por lo que sería de interés estudiar el plumón en otras especies de loros de tierras altas y ver si éstas presentan características similares a las observadas en *H. fuertesi*.

El aumento en la masa de los polluelos de la Cotorra Aliazul alcanzó sus valores máximos durante la primera mitad de su fase de cría (Tabla 1), lo que concuerda con lo observado en otros psitácidos neotropicales como *Myiopsita monachus catita* (Navarro & Bucher 1990) y *Amazona finschi* (Salinas-Melgoza 1999), que al igual que *H. fuertesi,* también presentan un descenso en el peso durante la segunda mitad de la fase de cría. De hecho, la disminución en el peso de los polluelos días antes de salir del nido ha sido observada no sólo en varias especies de psitácidos (Navarro & Bucher 1990, Aramburú 1997, Salinas-Melgoza 1999, Masello & Quilldfeldt 2002), sino también en diversos órdenes de aves (Ricklefs 1968a). Esto puede atribuirse a periodos de inanición, a una disminución en el tamaño de los órganos digestivos o a la alta energía que requiere el crecimiento de las plumas (Ricklefs 1968a).

Una posible aplicación de los valores calculados de parámetros y curvas de crecimiento es estimar la edad de pichones de edad desconocida con base en su tamaño. Estudios en algunos psitácidos indicaron que las medidas del ala y del pico son más apropiadas para este propósito porque éstas no presentan un decrecimiento hacia el final del período de permanencia en el nido como lo hace la masa (Saunders 1986, Salinas-Melgoza 1999). En el caso de la Cotorra Aliazul, el valor de usar datos de masa para estimar la edad es también limitado debido a la disminución de la masa en días previos a la salida del nido. Además, como los pichones mantienen su masa asintótica por cerca de un mes (Fig. 6), el peso sólo permitiría una estimación muy aproximada de la edad. Por este motivo, el uso de otras variables sería más recomendable, aunque es importante notar que las curvas de crecimiento del plumaje (Fig. 4 y 5) no permitirían estimar confiablemente la edad durante la primera semana de vida pues, aunque estas curvas asignan valores para este período, en ese momento las plumas aún no han aparecido: mis datos y los de Quevedo *et al.* (2006) indican que el crecimiento de las primarias se dispara en la segunda semana. Por lo tanto, recomiendo que para estimar la edad de pichones de edad desconocida se utilicen los parámetros de crecimiento del pico o del peso (Fig. 3) durante la primera semana de crecimiento, y de las plumas primarias una vez éstas hayan aparecido, debido a que esta curva tuvo el mejor ajuste a los datos y a que su asíntota se alcanza sólo durante el segundo mes de crecimiento. De modo más general, mis observaciones (ver también Quevedo *et al.* 2006) indican que es posible distinguir a las aves que recientemente han abandonado el nido de las aves adultas por la coloración del pico.

AGRADECIMIENTOS

Este trabajo fue posible gracias al apoyo logístico y financiero de la Fundación ProAves de Colombia y su proyecto de Loros Amenazados de la Cordillera Central, financiado por la Fundación Loro Parque. Los pobladores de las fincas Guayabal y El Brillante me permitieron el ingreso y el estudio de la especie en sus predios, y el equipo de trabajo de la Reserva El Mirador fue un apoyo constante durante mi trabajo de campo. Enrique Zerda y Juan Carlos Verhelst me asesoraron convenientemente y María Isabel Moreno realizó valiosos comentarios al manuscrito. Agradezco especialmente a Adriana Rodríguez-Ferraro y a un revisor anónimo, quienes evaluaron este manuscrito y contribuyeron a un mejor aprovechamiento y presentación de la información.

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Recibido: 25 febrero 2007
Aceptado: 3 marzo 2009

USING NITROGEN-15 TO EXAMINE PROTEIN SOURCES IN HUMMINGBIRD DIETS

Uso de nitrógeno-15 para examinar las fuentes de proteína en las dietas de los colibríes

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ABSTRACT

Hummingbirds rely on the sugars in nectar to meet their high metabolic requirements, but most nectars are extremely low in nitrogen. As a result, the birds must also consume arthropods to meet their protein requirements. In many hummingbird species, males use nectar resources differently from females. I hypothesized that the sexes might also differ in their use of arthropods, because breeding females have higher protein requirements. I used $\delta^{15}N$ isotopes in feathers and blood to demonstrate that females feed at higher trophic levels than males and adults at higher levels than juveniles, respectively. Females captured during the breeding season were also feeding at higher trophic levels than those captured outside of the breeding season, though the sample sizes were small. I also found a slight but unanticipated increase in $\delta^{15}N$ values in feathers with elevation in one species.

Key words: Arthropods, tropical cloud forest, hummingbird, nitrogen isotopes.

RESUMEN

Los colibríes dependen de los azúcares del néctar para suplir su elevada demanda metabólica, pero la mayoría de los néctares son extremadamente pobres en nitrógeno. Como consecuencia, estas aves deben consumir también artrópodos para satisfacer sus necesidades proteicas. En muchas especies de colibríes, los machos y las hembras utilizan los recursos florales en forma diferente. Propuse que los sexos también podrían diferir en el consumo de artrópodos, porque las hembras tienen mayores demandas de nitrógeno durante la época reproductiva. Empleé isótopos $\delta^{15}N$ de plumas y sangre para demostrar que las hembras se alimentan en niveles tróficos más altos que los machos y que los adultos lo hacen en niveles más altos que los juveniles. Las hembras capturadas durante la temporada reproductiva también se alimentaron en niveles tróficos más altos que las capturadas fuera de la época de cría, aunque el tamaño de las muestras fue pequeño. También encontré un leve pero inesperado aumento en los valores de $\delta^{15}N$ en las plumas con elevación en una especie.

Palabras clave: Artrópodos, bosque de niebla tropical, colibrí, isótopos de nitrógeno.

INTRODUCTION

Hummingbirds are best known as nectarivores, but also supplement their diet with arthropods and probably some fruits. They rely on sugar-rich nectars, which are extremely low in nitrogen, to meet their high metabolic requirements. These birds have a suite of adaptations to their nitrogen-poor diets, including lowered nitrogen demands (McWhorter et al. 2003, Tsahar et al. 2005) and specialized bacteria in their guts to recycle nitrogen (Preest et al. 2003). Such adaptations to conserve nitrogen imply an important role for protein sources in hummingbird diets. Meeting protein needs may figure in their behavioral and physiological adaptations more than has been recognized. Indeed, the availability of arthropods may determine the timing of breeding in dry tropical forests (Poulin & Lefebvre 1997).

Compared to females, male hummingbirds typically spend more time defending their territories (Chai et al. 1996, Temeles et al. 2002, Van Dooren et al. 2004), less time tending the nest (Baltosser 1996), and do not feed the young (Stiles 1995). The sexes may also employ different foraging strategies to reduce intraspecific competition (Temeles et al. 2002). Although these gender differences are well-studied in relation to nectar resources, there is very little information on arthropod foraging. One study in the Colombian Andes found female hummingbirds are more likely to have spiders in their guts than males (Rico-G. 2005). Female birds of other species have been found to have higher protein requirements than males (Moore et al. 2000) and metabolize more protein (Durant et al. 2000) during egg production. Thus, I hypothesized that female hummingbirds might differ from males in their selection of arthropods, because of their likely higher protein requirements for breeding. Furthermore, I hypothesized that juveniles' diet might be more similar to females', because they also face high nitrogen demands for growth.

This study compares the arthropod component of diet among three hummingbird species common in the Eastern Andes, and between genders, age classes, and seasons in the two of these species that are sexually dimorphic. *Adelomyia melanogenys* (Speckled Hummingbird) is a small, monomorphic (though males are usually larger than females), short billed generalist (Altshuler 2006). The other two species are strongly dimorphic, so their sexes can be readily distinguished in the field. *Heliodoxa leadbeateri* (Violet-fronted Brilliant) is stocky and aggressively territorial (Altshuler, 2006), and shows marked sexual dimorphism not only in plumage, but also in the males' greater size and slightly shorter, straighter bills. In *Coeligena torquata* (Collared Inca), the sexes are also readily distinguished by plumage. Males are slightly larger but on average, have shorter bills. Their behavior has not been classified, but a Peruvian congener was described as a "filcher" (Altshuler 2006). Filchers steal nectar from territories defended by other birds. In Colombia, males sometimes defend territories based on preferred flowers if these are in sufficiently dense aggregations; at other times they may trapline or, more rarely, filch (F. G. Stiles, pers. comm.). Birds that employ stealing strategies regularly get into to aggressive interactions (unlike trap-lining hummingbirds which make repeated visits to a series of plants), but almost never as aggressors.

It is easy to see hummingbirds catch arthropods on occasion, but difficult to gather systematic data for prolonged periods. In fact, there are no published data sets that quantify gender differences in arthropod foraging behavior. Stiles (1995) did not demonstrate any sex-specific arthropod foraging in a long-term study at a lowland rainforest site in Costa Rica. Furthermore, nectar leaves almost no trace in the digestive tract, so gut analyses of hummingbirds cannot reveal information on nectar use, and foraging observations are biased toward easily-observed flower visits (Stiles 1995). Given this difficulty in evaluating protein sources via direct observations, isotopic analysis can provide an alternative (Post 2002).

Nitrogen enters ecosystems primarily from the atmosphere, where the stable isotope $\delta^{15}N$ is 0.366% of total N. Once incorporated into biological systems, metabolic pathways favor ^{15}N during each step of protein synthesis. Therefore, top predators have appreciably higher $^{15}N:^{14}N$ ratios than autotrophs. In general, the change in $\delta^{15}N$ between trophic levels is 3.4±1.3‰ (Post 2002). Thus, $\delta^{15}N$ (defined as $[(R_{SAMPLE} - R_{STANDARD})/R_{STANDARD}]*1000$, where R_{SAMPLE} is the measured ratio of $^{15}N:^{14}N$ in the sample, and $R_{STANDARD}$ is the known ratio of $^{15}N:^{14}N$ in air) can be used to evaluate the relative importance of different foods in an animal's diet because higher $\delta^{15}N$ values imply feeding at higher trophic levels. For instance, this method has successfully distinguished bats that feed primarily on fruit from bats that consume more arthropods (Herrera et al. 2001), and revealed that tropical passerines rely more heavily on protein from fruits than protein from insects when fruits are most abundant (Herrera et al. 2005).

In this study, I rely on an important difference between the way dietary nitrogen is incorporated in feathers, and the way it is incorporated into whole blood. Feathers are inert material, their composition permanently fixed at growth. Blood, on the other hand, reflects the animal's diet in the 5-10 days before sampling. In addition, the $\delta^{15}N$ signatures differ slightly between feathers and blood simply because of the metabolic pathways involved in the production of each tissue. Keratin in feathers has a slightly higher $\delta^{15}N$ signature than blood even in laboratory experiments where birds are fed a constant diet (Hobson & Bairlein 2003).

Because they require nitrogen to supplement their largely nectar-based diet, nearly all hummingbirds forage for arthropods in one fashion or another, primarily by hover-gleaning, or by hawking (Stiles 1995). The prey taken by hover-gleaning might include small spiders and prey stored in spider webs, whereas hawking behaviors will only capture flies. Because spiders feed at a higher trophic level than most flies, their tissues are expected to contain a higher proportion of $\delta^{15}N$. That higher proportion should be reflected in the tissues of hummingbirds that consume a large fraction of spiders, as was observed in female hummingbirds in Colombia (Rico-G. 2005). I determined the $\delta^{15}N$ ratio and total nitrogen content of flies and small spiders, and then compared that to the $\delta^{15}N$ in hummingbird feathers.

MATERIALS AND METHODS

STUDY AREA.- Sangay National Park, on the western edge of the Amazon basin, extends from the peaks of some of Ecuador's tallest volcanoes into the lowlands of the tropical rainforest. It represents some of the most intact contiguous forest remaining on the eastern slope of the Andes in Ecuador. My research sites were along the new road which bisects the park or the backcountry trail to the Sardinayacu Lakes (Fig. 1). The precise locations were Purshi, 2500 m (2°12'S, 78°23'W); Lago, 1750 m (2°04'S, 78°13'W); Primero, 1550 m (2°05'S, 78°11'W; and Nueva, 1350 m (2°06'S, 78°09'W). At each site, I cleared net lanes opportunistically, near hummingbird flowers or along small ridges. On each visit, I captured birds in mist nets (12 m, 4 shelf, 32 mm mesh). Each sampling day, I ran 10-15 nets for approximately 8 hours, beginning at sunrise. Because capture rates dropped precipitously even on the second day, I tried to net no more than three days per site per month.

FIELD METHODS.- I observed several species of hummingbirds visiting tiny spider webs on a rock wall near my field site, so I collected arthropods from the webs and stored them in 99% ethanol for isotopic analysis. In most cases, it was easy to find and collect the spider. I occasionally found remnants of tiny flies in the webs, but never sufficient to sample. I collected live flies and microhymenopterans from near plants where I saw birds perched. I also collected fruit (blackberry) and pollen from *Fuchsia* sp. I collected only small arthropods, and it was necessary to homogenize all the samples to achieve sufficient mass for the elemental analyzer.

Between July and October, 2004, in April 2005, and between July and October, 2006, I captured 22 *A. melanogenys*, 28 *C. torquata*, and 24 *H. leadbeateri* and collected two retrices and ~ 75uL of blood from a clipped claw from each bird (IACUC protocol A126-06-04). Juveniles were identifiable by minute striations along the length of their bills. Also, as with other species of *Heliodoxa* (cf. Ridgway 1911), juveniles of *leadbeateri* have prominent buffy to rufous borders to the malar stripe, which are visible even through binoculars. I stored the retrices in envelopes at ambient temperature and preserved the blood in 1.5 mL tubes with 99% ethanol until analysis.

I attempted to make direct observations of arthropod foraging by hummingbirds, but met with limited success. I was only able to record foraging activities by *H. leadbeateri* and *C. torquata* 12 and 7 times, respectively. For half of the *H. leadbeateri* observations, I was unable to determine the bird's sex.

LABORATORY AND STATISTICAL METHODS-. I cleaned the feathers of surface oils using 2:1 chloroform: methanol solution, and then dried them overnight in a fume hood. I then cut 1.00 mg

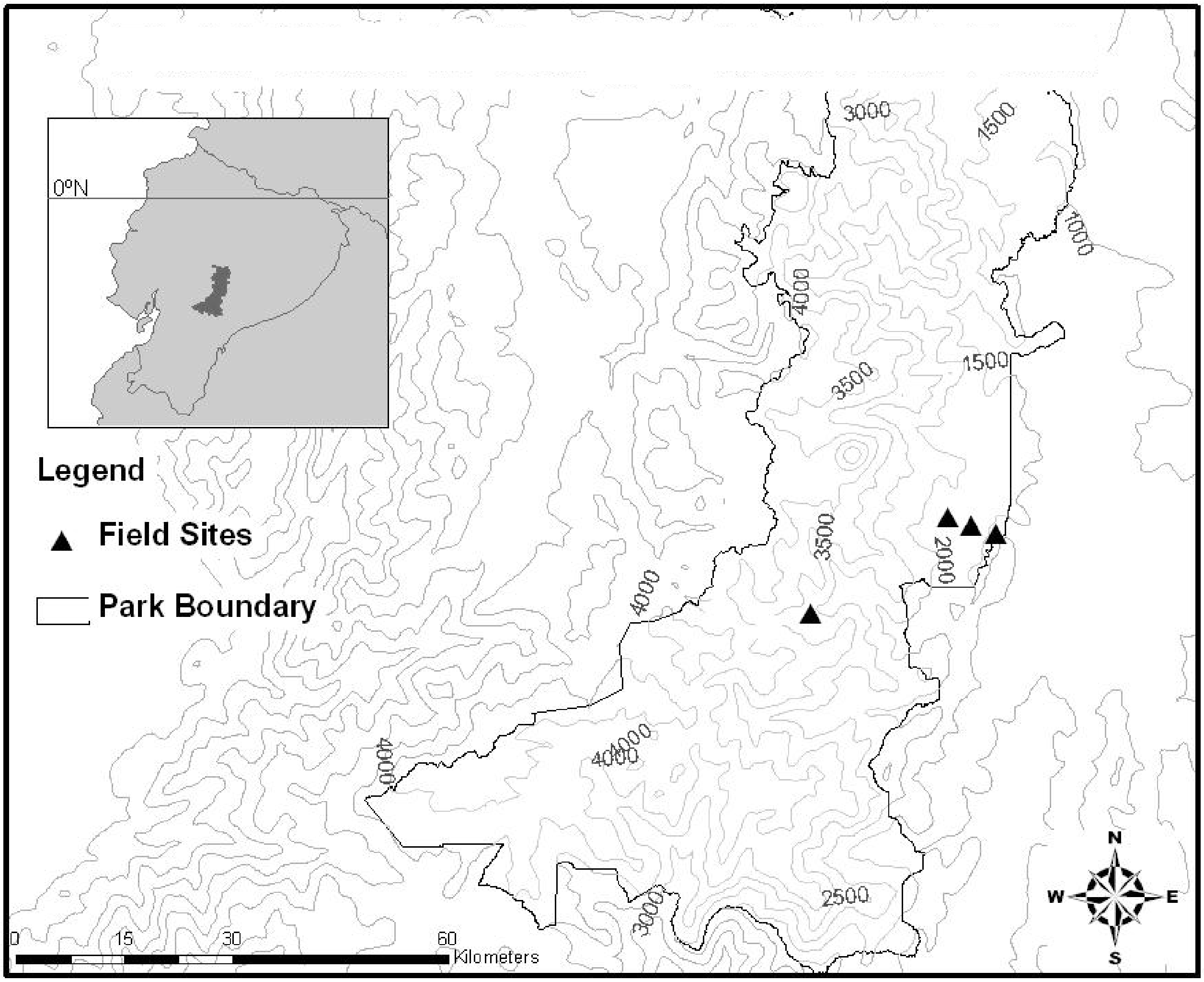

Figure 1. Study sites in Sangay National Park, on the eastern slope of the Andes in Ecuador.

samples from the feather vane and packaged them in tin cups. I freeze-dried the blood and arthropods in a lyophilizer overnight, and then weighed out 0.35 mg samples. The samples were run in the Duke Environmental Stable Isotope Laboratory on a Carlo Erba Elemental Analyzer Mass Spectrometer with precision of duplicate samples ± 0.11‰. Standards were composed of international reference materials IAEA N_2, and Duke University internal standards, Duke Cellulose, Duke Sucrose, Duke Urea, and Costech acetanilide. The laboratory reports precision as generally ± 0.2‰ relative to external standards and a little better relative to internal standards.

For data analysis, I used parametric approaches and R software. To compare among sub-specific groups, I used a two-way fixed-effects analysis of variance with interaction, which assumes a normal distribution. The data violated the rule of thumb that no group should have a standard deviation more than double that of another (juvenile *A. melanogenys* and *C. torquata*), but since the sample sizes were so small, I considered this acceptable. I used paired t-tests (with pooled variance) to compare blood to feather values, and to compare female blood values between seasons. Since I had strong predictions about both of these relationships (that feathers and breeding season blood samples would be higher), I used a one-tailed hypothesis test. Finally, I also used linear models to examine the relationship between blood and feathers, and the effect of elevation on δ^{15}N values in feathers.

RESULTS

PROTEIN SOURCES.- The spiders I collected contained both a higher concentration of nitrogen and a higher $\delta^{15}N$ than flies (Table 1).

Table 1. Spiders had both higher percent nitrogen composition and a higher $\delta^{15}N$ value than other potential sources of hummingbird dietary protein at 2500 m elevation. Because samples were small, and material was homogenized for analysis, error estimates are unavailable.

	N	**$\delta^{15}N$**
Spider	14.6 %	7.4‰
Flies	11.0%	3.5‰
Fuchsia sp. Fruit	0.9%	4.0‰
Fuchsia sp. Pollen (n = 2)	3.7±1.9%	-5.1±4.4‰

EFFECTS OF SPECIES, AGE AND GENDER.- $\delta^{15}N$ of tail feathers varied by species, age class, and gender (for the species which I was able to sex in the field). I compared the effects of species and age class on feather $\delta^{15}N$ for all three species. An analysis of variance yielded a significant main effect for both species, F (1,74) = 12.7, p<0.001, and age class, F(1,74) = 6.2, p = 0.015, such that $\delta^{15}N$ was significantly lower for juveniles (mean = 6.34‰, SD = 2.10) than for adults (mean = 7.53‰, SD = 1.24; Table 2). I was unable to compare sexes in the monomorphic *A. melanogenys*, but feathers from female *C. torquata* showed significantly higher $\delta^{15}N$ levels (one tailed t_{20}=1.73, p=0.05) than males. There was weaker evidence for a difference between sexes in *H. leadbeateri* (one tailed t_{16}=1.63, p=0.06).

Table 2. ANOVA results showing primary effects indicate that both species and age class had a significant effect on $\delta^{15}N$ values of hummingbird feathers.

Effects	**SS**	**df**	**MS**	**F**	**P**
Species	42.89	2	21.45	12.69	<0.001
Age class	10.44	2	10.44	6.18	0.015
Interaction	3.76	2	1.88	1.16	0.334
Residuals	118.8	70	1.69		

Previous studies of trophic position have examined $\delta^{15}N$ in blood rather than in feathers (Herrera et al. 2003, Herrera et al. 2006), so I examined the relationship between $\delta^{15}N$ in blood and feathers in my data. Because feathers have slightly higher $\delta^{15}N$ values, even in birds fed a consistent diet, I expected my feather $\delta^{15}N$ values to be slightly higher than the blood $\delta^{15}N$ values from previous research. Although I was unable to collect and analyze blood from each individual used in the feather study, I had both blood and feather data for a total of 30 hummingbirds of a variety of species. In these birds, the mean $\delta^{15}N$ in blood was 2.12‰ lower than that of feathers (paired t_{30}=-10.23, p<0.001). This is comparable with laboratory values of a 1.7‰ difference between blood and feathers in *Sylvia borin* (Garden Warblers; Hobson & Bairlein 2003). Regression analysis comparing blood and feathers from given birds showed a highly significant relationship ($F_{1,29}$=62.0, p=.0004) (Fig. 2). Blood samples from the present study ranged from 5.03‰ for a juvenile *A. melanogenys* to 8.24‰ for an adult *C. torquata*. However, values of $\delta^{15}N$ in feathers and blood were generally in the same range as those of spiders.

EFFECT OF SEASON.- Because samples sizes of blood were so small, I used feathers for most comparisons, and blood $\delta^{15}N$ only to compare females captured during breeding and non-breeding seasons. This comparison could only be done with blood, because it required a tissue that integrated values over a short period of time, and offered current values. Because feathers are inert, they capture information only from the period during which they were grown. Juvenile hummingbirds were common in the nets during October and November. Blood samples from female *H. leadbeateri* had lower $\delta^{15}N$ during the months that no juveniles were sighted (5.68 ± 0.26‰) than when there were juveniles present (6.77 ± 0.08‰). The difference was significant (one tailed t_9=3.44, p=0.003 $n_{breeding}$ = 5, $n_{non-breeding}$= 4). Molt was most common in October, which was immediately after breeding.

EFFECT OF ELEVATION.- There was a significant, though noisy effect of elevation on $\delta^{15}N$ *in A. melanogenys* ($F_{1,09}$=7.716, p=0.01) (Fig. 3).

DISCUSSION

There are clearly some differences in the diet of the

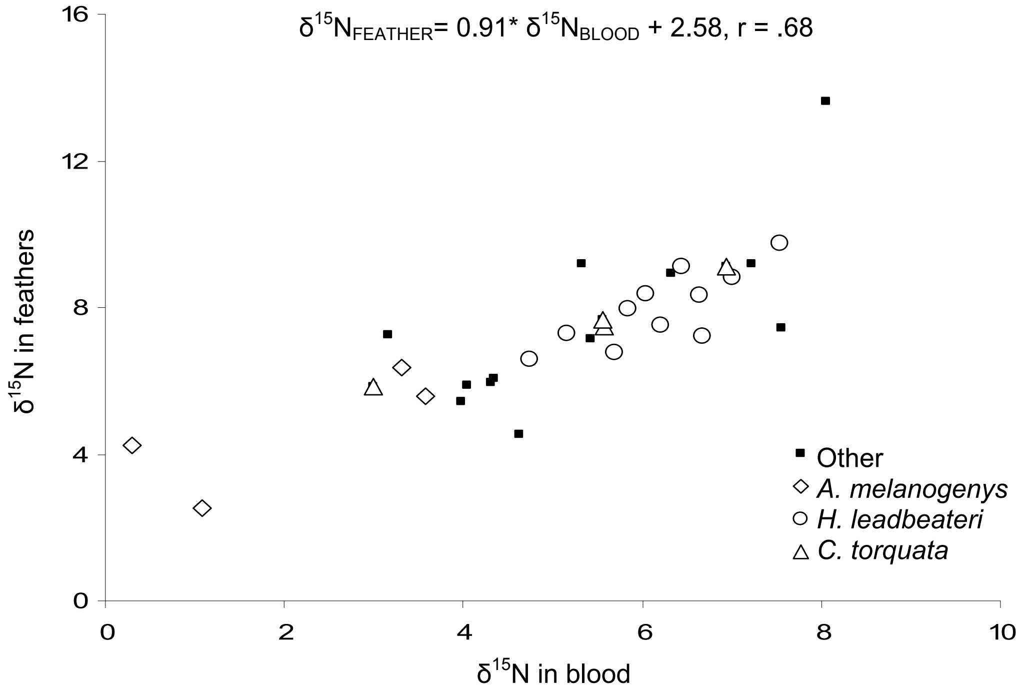

Figure 2. Feather δ^{15}N values of Andean hummingbirds averaged 2.12‰ higher than blood. "Other" designates hummingbird values from species in addition to the focal species.

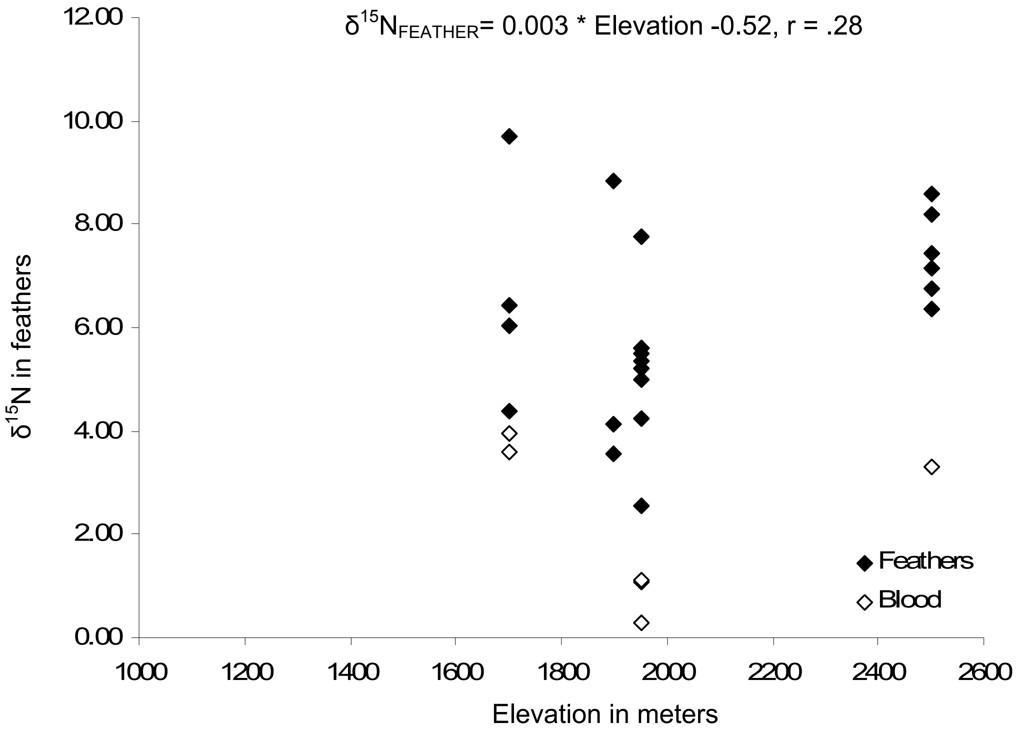

Figure 3. δ^{15}N in *A. melanogenys* feathers bore a slight but significant relationship to elevation ($F_{1,20}$=7.716, p=0.01). Blood values shown for comparison. The possibility of such an effect should be considered in future studies.

smaller, lighter, shorter-billed *A. melanogenys* compared to *H. leadbeateri* and *C. torquata. A. melanogenys* individuals are probably using a wider variety of protein sources, perhaps incorporating some nitrogen from fruit. The differences between the two dimorphic species were minimal, though the behavior of *H. leadbeateri* might have led us to expect lower $\delta^{15}N$ values since it is the more territorial of the two species, which is correlated with higher burst power in flight (Altshuler 2006). Higher burst power generally entails less ability to hover (Chai et al. 1996), so we might have expected that *H leadbeateri* would prefer flying prey to that obtained by raiding webs, thus consuming fewer spiders and having lower $\delta^{15}N$. This analysis failed to detect such a difference.

The results suggest that female hummingbirds feed at a higher trophic level than males (Table 3), which is consistent with a recent behavioral study of Colombian hummingbirds that found females relying more heavily on spiders than males of the same species (Rico-G. 2005). The differences in that study were especially marked in *Coeligena helianthea*, a congener of *C. torquata*, one of the species included in my study. Isotopic analysis deals only with assimilated protein (Herrera et al. 2005) in tissues, so that a higher $\delta^{15}N$ does not imply more total protein in the diet. However, spiders are both richer in protein and have higher $\delta^{15}N$ than flies, so female hummingbirds are likely assimilating more protein (Table 3). Moreover, previous studies examining isotopic variation have only discriminated among species of different guilds (Herrera et al. 2003). The present work demonstrates that ^{15}N can also be used to discriminate within the rather narrow guild of nectarivores, and even further, within species.

Sexes may differ in their prey selection because the trade-offs of consuming volant vs. non-volant arthropods play out differently for male and female hummingbirds. Males generally have narrower wings, even in species that have almost no sexual dimorphism (Stiles 1995 and pers. comm.). Their narrower wings are thought to give them greater maneuverability and more powerful flight, which is useful in territory or mate defense, but makes hovering more difficult and more energetically demanding (Chai et al. 1996). Hence males may be eating more volant arthropods because they are less costly to catch. Aerial foraging strategies may also be less disruptive to maintaining vigilance of their territories. On the other hand, females have broader wings and they also face higher nitrogen demands. Therefore, hovering and surface gleaning (and thereby taking more spiders) might be more energetically efficient for females than males.

The higher $\delta^{15}N$ values in the blood of females during months when juveniles were also present indicates a breeding season shift in arthropod diet, possibly in response to the high nitrogen demands of reproducing. This intra-annual difference in diet underscores the importance of protein sources to the hummingbirds. The results are consistent with the hypothesis that demands of protein synthesis during breeding can result in generalized sex differences in avian resource use.

Finally, I hypothesized that juveniles would have $\delta^{15}N$ levels comparable to those of females because they also face high protein requirements for their growth. Instead, they generally showed lower values of $\delta^{15}N$ than adults of either sex. This might be because juveniles lack the skills or stamina to forage on the same prey as adults, so they forage for different prey on different substrates.

The results of my research could be confounded by three things: other sources of nitrogen, metabolic or physiological differences between genders, or other unexplained effects. The role of other sources of nutrients, such as pollen and fruit, is not likely to be

Table 3. Female hummingbirds tended to have higher $\delta^{15}N$ values in their feathers. The $\delta^{15}N$ values were lower in juveniles. Values are Mean ± 1 SD, (sample size).

Species	Adults	Males	Females	Juveniles
A. melanogenys	6.53 ±1.2‰ (16)	N/A	N/A	5.03±2.12 ‰ (7)
H. leadbeateri	7.95±0.96‰ (21)	7.39±0.99‰ (9)	8.09±0.97‰ (12)	7.22±0.96 ‰ (4)
C. torquata	7.84±0.94‰ (22)	7.55±1.04‰ (12)	8.24±0.82‰ (10)	7.55±1.94 ‰ (5)

great in the diet of any hummingbird species. Pollen is probably too well protected to be digestible by hummingbirds' rather weak digestive system (van Tets & Nicolson 2000), and fruit has generally such a low total nitrogen content that it is incapable of contributing very much protein to a hummingbird's diet (Levey & Martínez del Río 2001).

Gender differences are unlikely to be caused by metabolic differences, and physiological differences between genders have not been studied in relation to protein, although they have been examined in relation to sugar digestion (Markman et al. 2006). Both body size (Sweeting et al. 2007, Jennings et al. 2008) and metabolism (MacAvoy et al. 2006, Jennings et al. 2008, Martínez del Río et al. 2009) can affect nitrogen isotopes. However, in captive studies of other birds, there has been no indication that ^{15}N assimilation differed between genders (Pearson et al. 2003). Some captive studies can be difficult to extrapolate to natural environments, but metabolic pathways are unlikely to be affected by captivity.

Because this is a relatively new field, there is also a possibility of other unexplained effects. A more precise baseline of δ^{15}N for the ecosystem would strengthen the conclusions presented here. For example, if the spiders I sampled were actually representative of the higher trophic levels of prey items, we would have expected feather values to have δ^{15}N values 2.4 ‰ higher than the arachnids, rather than similar values. Clearly, the full explanation of sources of assimilated protein sources for these hummingbird communities is more complex than this research could detect. In fact, it is difficult to account for all of the sources of variation even in much better-studied systems (Daugherty & Briggs 2007). Further research should pay careful attention to achieving a representative sample of all potential protein sources.

In addition to the hypotheses this study was designed to address, I found an unanticipated direct relationship between elevations and feather δ^{15}N for *A. melanogenys* (the species with the widest altitudinal range). Such an effect has not been reported (much less explained) by any study using N-15. The present study was not designed to test for an effect of elevation. Nevertheless, this relationship should be examined in future studies that include samples form a broad elevation range to determine whether it might represent a general phenomenon. Because I did not determine the sex of the *A. melanogenys* I captured, it is possible that my small sample of this species at the highest elevation consisted of only females. If female *A. melanogenys*, like the females of the other species, have higher δ^{15}N values, then the relationship to elevation might reflect different gender ratios at different sites, resulting from partial migrations. Alternatively the selection of arthropods possibly might vary with site, and affect the δ^{15}N of assimilated protein. It is therefore possible that this relationship might be an artifact of sampling, but it might also have a biogeochemical explanation. In any case, it is important to report and understand, since such a relationship could confound results of other studies. Very few studies have examined the effect of elevation on δ15N, and none anywhere near this system, but changes in soil δ^{15}N, total N, and gravimetric water content have been found to affect leaf δ^{15}N elsewhere (Bai et al. 2009).

Stable isotope analysis offers novel insights into the diets of nectarivorous birds, and overcomes some of the challenges that have plagued behavioral studies, like the difficulty in getting gender-specific and arthropod foraging data. In this paper, I have shown strong differences between the diets of male and female hummingbirds, which I suggest are the product of both physiological constraints of sexual selection, and the protein requirements of breeding. These differences have been suggested previously, but have not been convincingly confirmed until this paper.

ACKNOWLEDGMENTS

Special thanks are due to my intrepid and snake-savvy field assistants, Fanny and Maria Paucar, and Mery Juina. My husband and field assistant, Brian Norris provided both brawn and moral support. Jonathan Karr gave good advice and good company in the Duke Isotope Laboratory. Further support was generously offered by The US Fulbright Program and the Ecuadorian Fulbright Commission, Duke's Giles Keever competition for lab work, and the Latin American Studies Program at Duke University, both through their internal grants and via administration of a Foreign Language Acquisition Scholarship. F. G. Stiles and Marion Adeney made many helpful comments on earlier drafts. Alejandro Rico generously shared his unpublished data, commented on the manuscript, and translated the abstract.

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Recibido: 30 julio 2008
Aceptado: 10 junio 2009

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 specificially 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

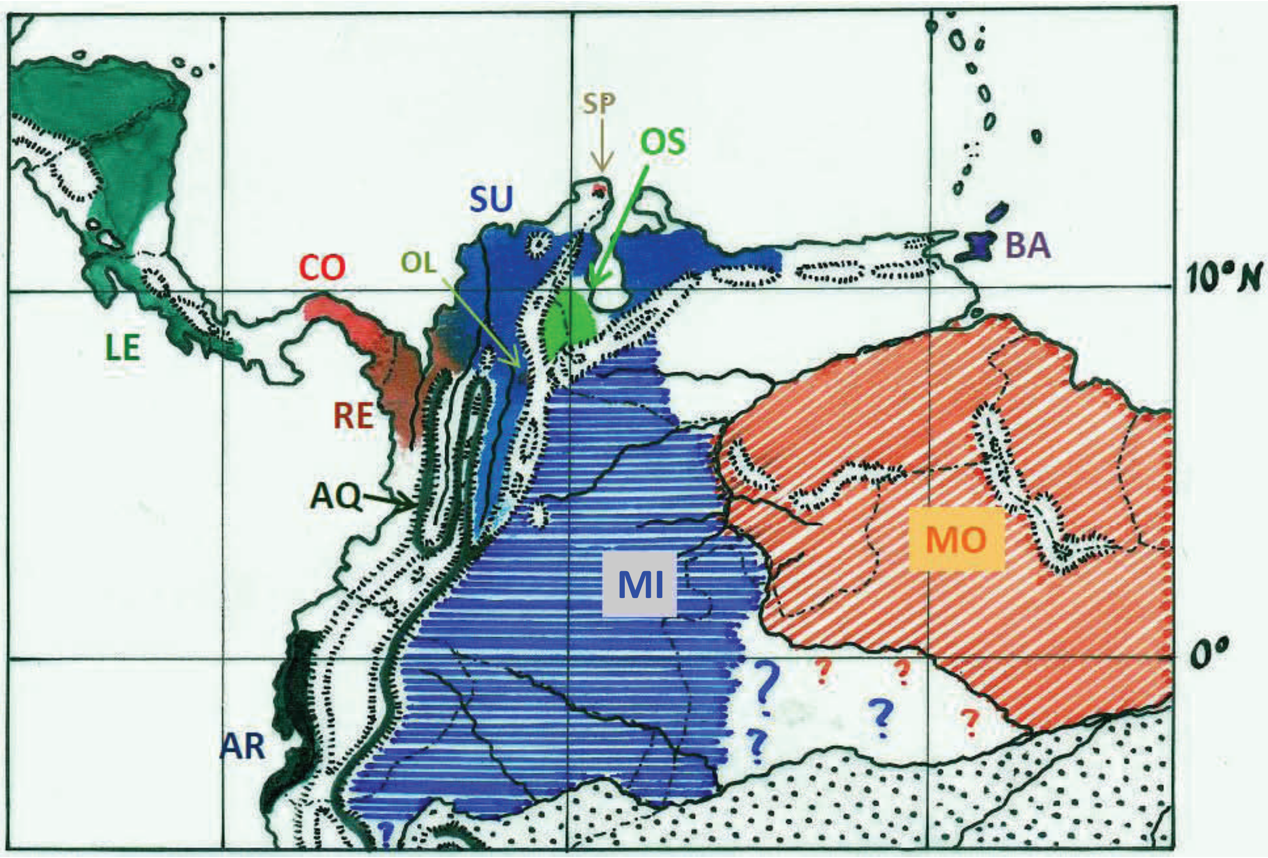


Figure 1. Distributions of the forms of the "*Momotus momota*" complex treated in this study: From northwest to southeast, LE = *lessonii*; CO = *conexus*; RE = *reconditus*; SU = *subrufescens*; OL = *olivaresi*; SP = *spatha;* OS = *osgoodi*; BA = *bahamensis*; AQ = *aequatorialis*; AR = *argenticinctus*; 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

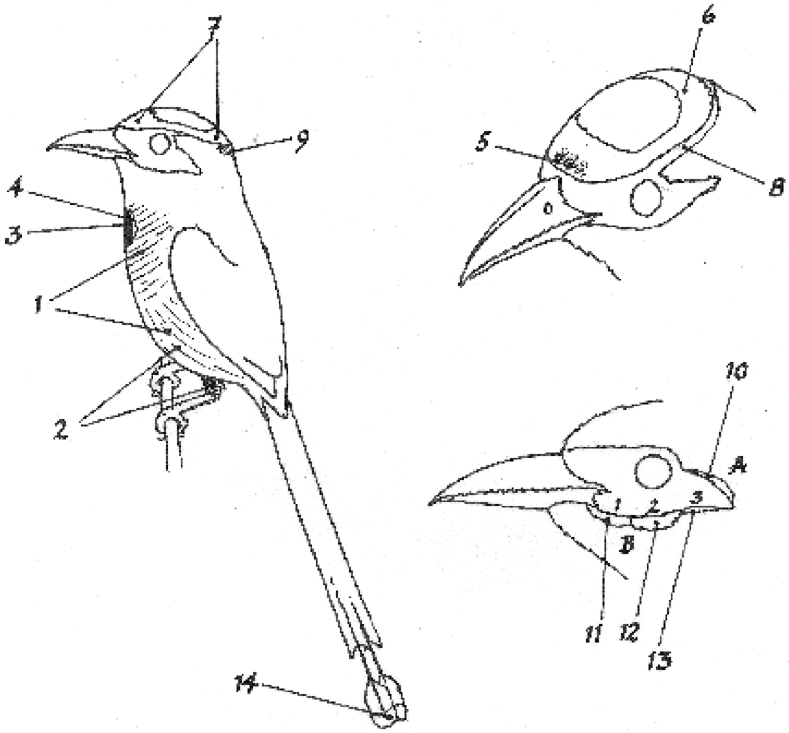


Figure 2. Summary of characters of plumage pattern useful for distinguishing between taxa of the "*Momotus momota* complex". 1: color contrast between chest and abdomen; 2: color contrast between thighs and flanks; 3: number of black feathers, and 4: extent of blue borders, on the "stickpin" of the center 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

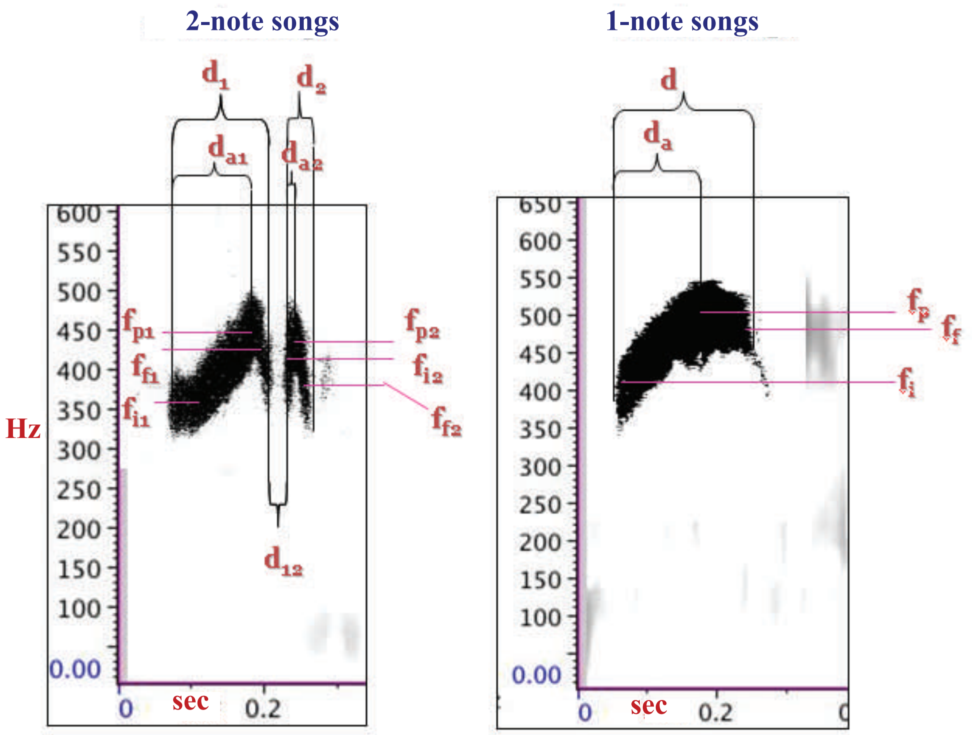


Figure 3. Temporal and frequency parameters measured in one- and two-note primary songs of members of the *Momotus momota* complex. **d**=duration (in milliseconds or seconds) **f**=frequency (in Hz). $\mathbf{d_a}$=duration of the initial ascending portion of a note; $\mathbf{f_i}$=initial, $\mathbf{f_p}$=peak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

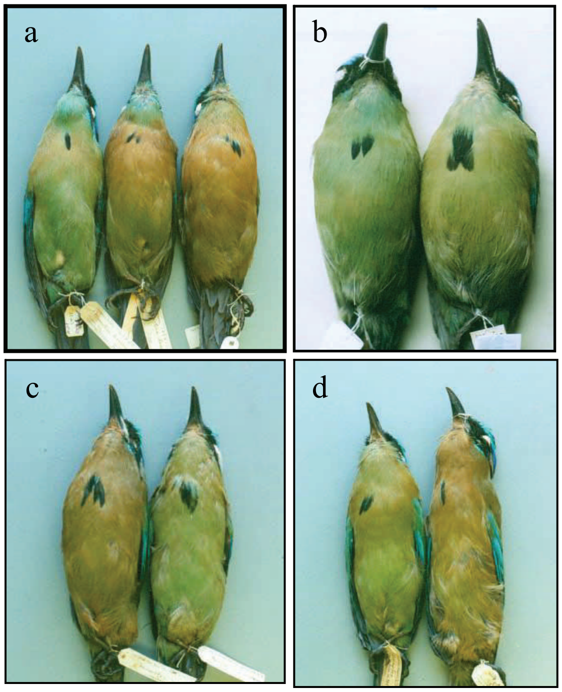


Figure 4. Variation in ventral coloration in four taxa of the "*Momotus momota* complex". **a.** *lessonii*; **b.** *aequatorialis*; **c.** *microstephanus*; and **d.** *momota.* Note the high degree of variation in *lessonii*; at the other extreme is *aequatorialis,* which is always quite green; *momota* and *microstephanus* are intermediate.

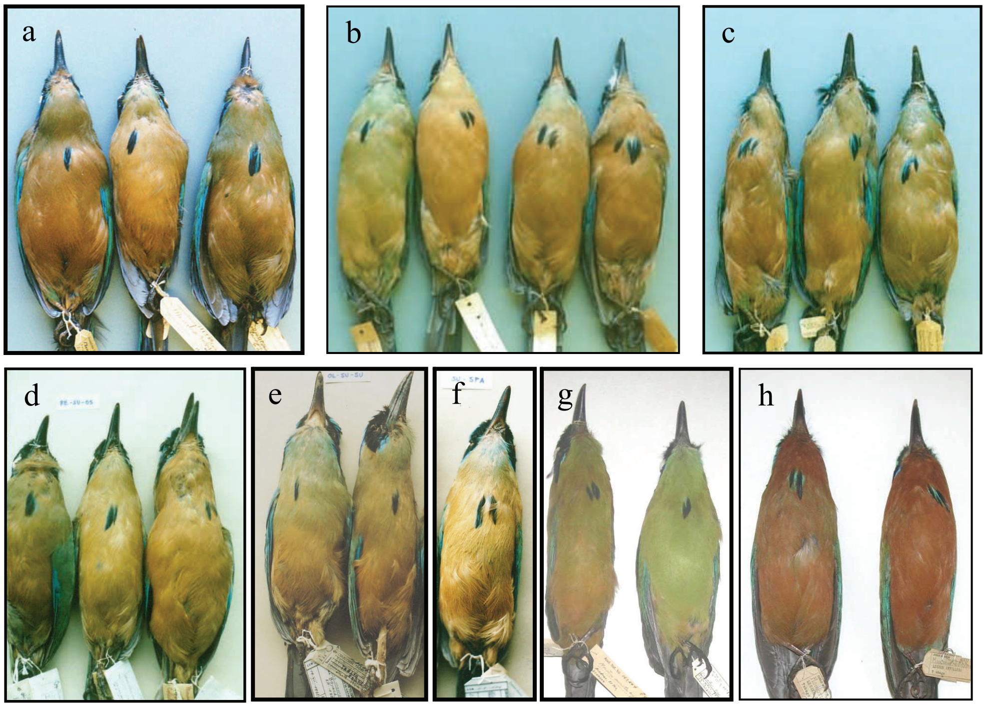


Figure 5. Ventral coloration in the "*subrufescens* group". Note that in all taxa, the chest is as green or greener than the abdomen**. a.** three specimens of *conexus*; **b.** four specimens of *subrufescens* from Bonda, Dept. of Magdalena, N Colombia, showing the degree of variation frequent in taxa 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.

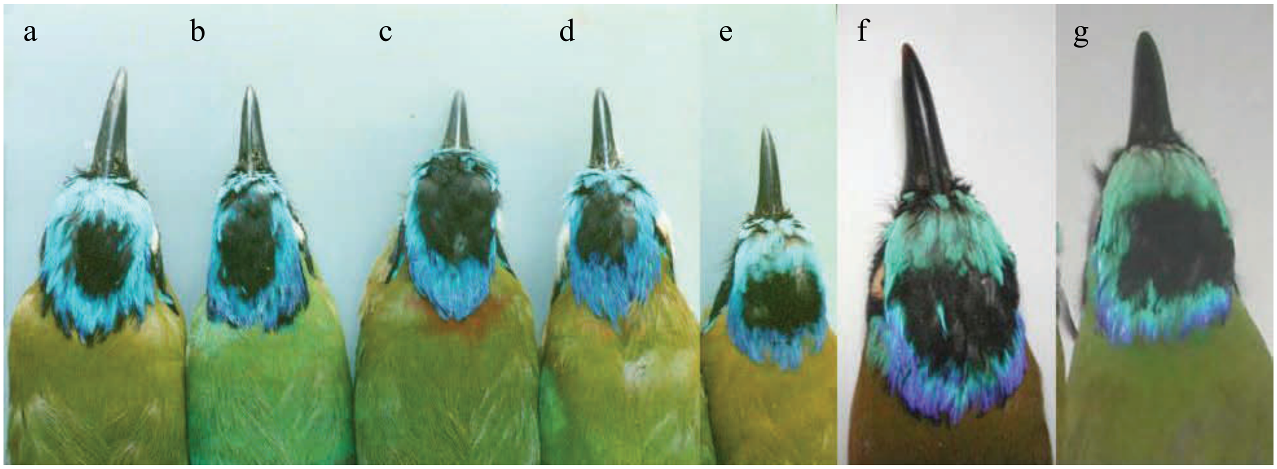


Figure 6. Crown patterns of several taxa of the *Momotus momota* complex. **a.** *aequatorialis*: note even width and uniform color all around the diadem, black posterior border; **b.** *lessonii*: similar to preceding but more violet in posterior part of diadem; **c.** *momota*: posterior part of diadem 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.

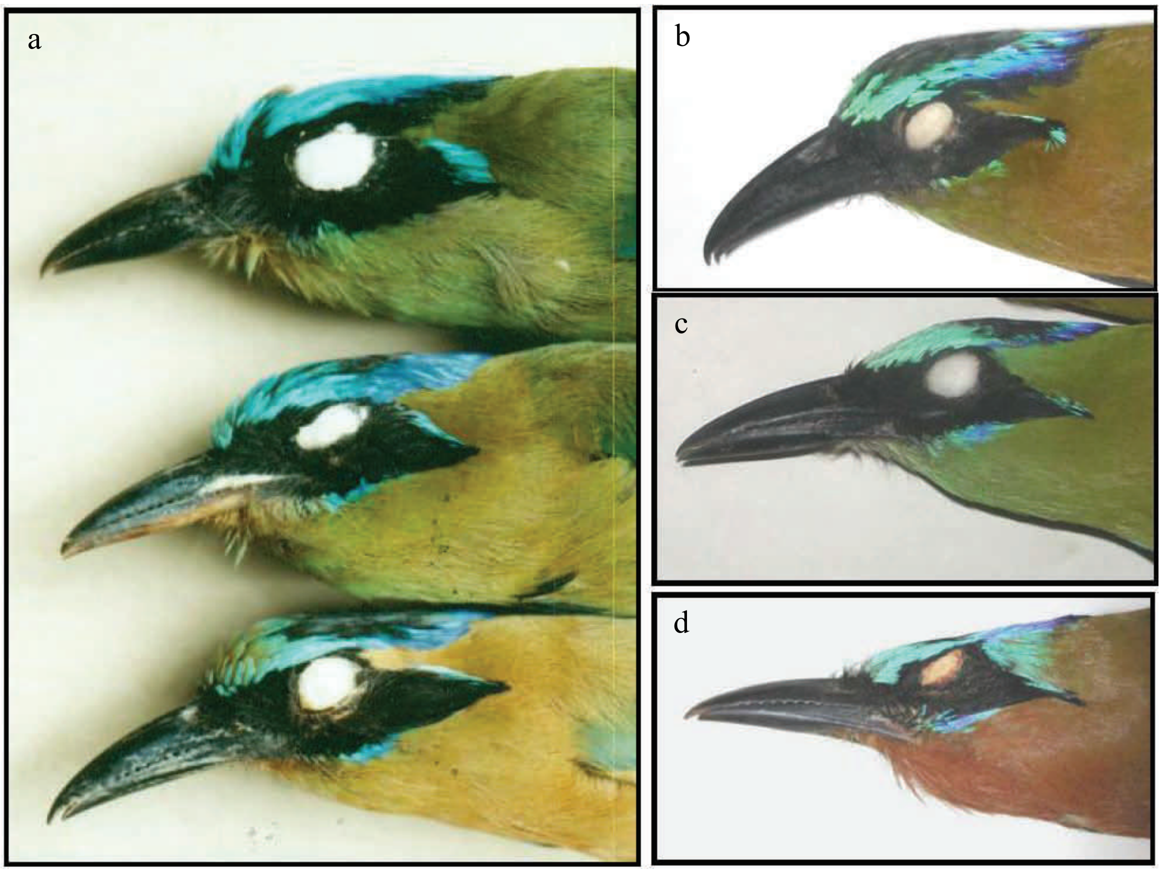


Figure 7. Masks of several taxa of the *Momotus momota* complex. **a.** top to bottom: *aequatorialis, microstephanus, subrufescens*; **b.** *lessonii*; **c.** *argenticinctus*; **d.** *bahamensis*. Note poor development of lower (B) portion of border, conspicuous upper (A) portion in *aequatorialis*; 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.

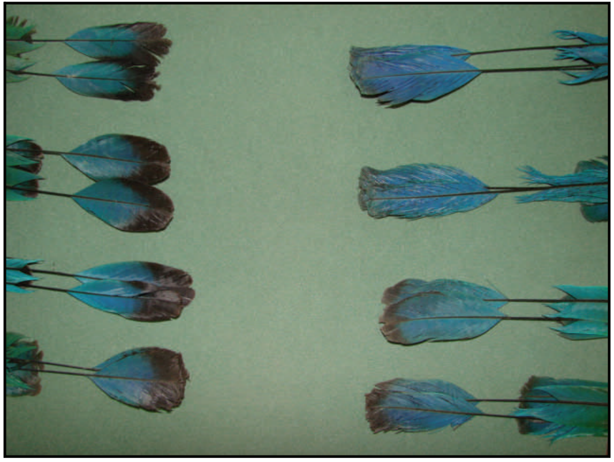


Figure 8. Racquets of several taxa of the *Momotus momota* complex. **Left, from top to bottom:** *reconditus*; *subrufescens*; *spatha*; *osgoodi***.** Note the clear-cut black terminal portion and tendency towards a broader, more spatulate shape in all. **Right, top to bottom:** two tails of *aequatorialis*; 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.

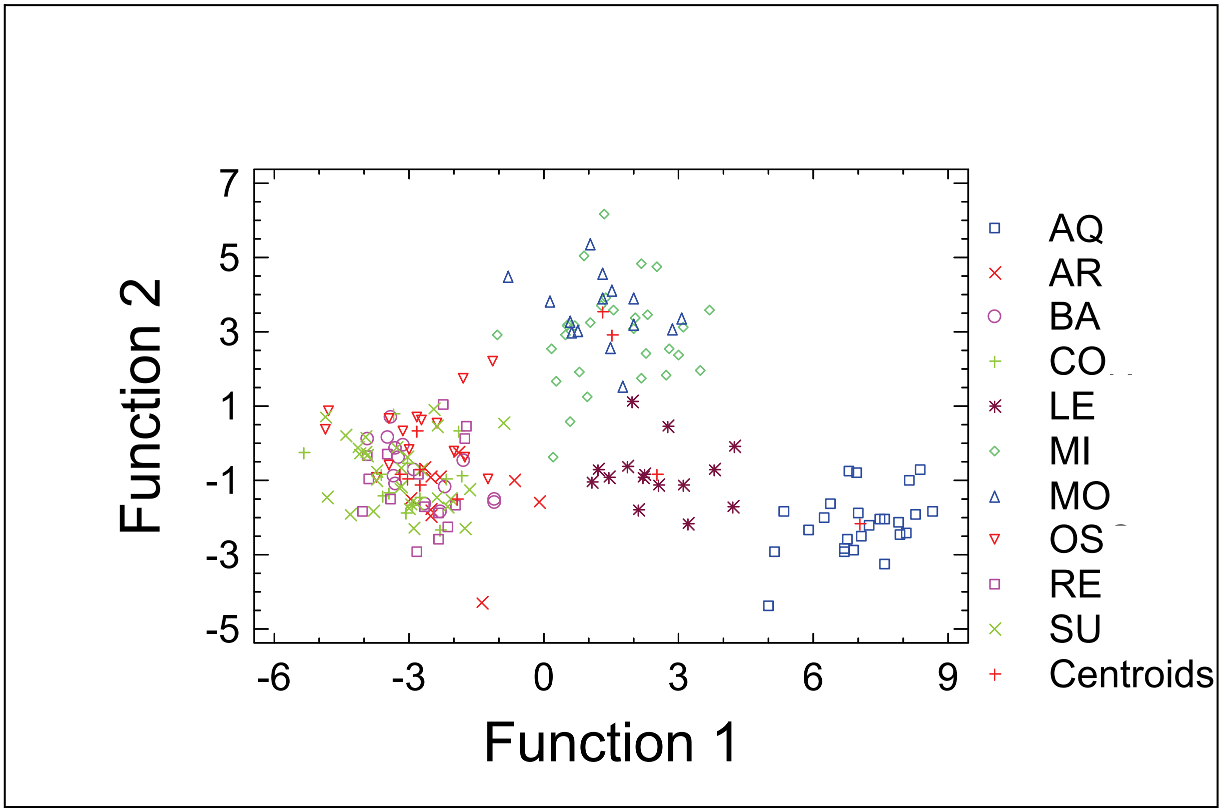
Analyses of plumage color and pattern

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,



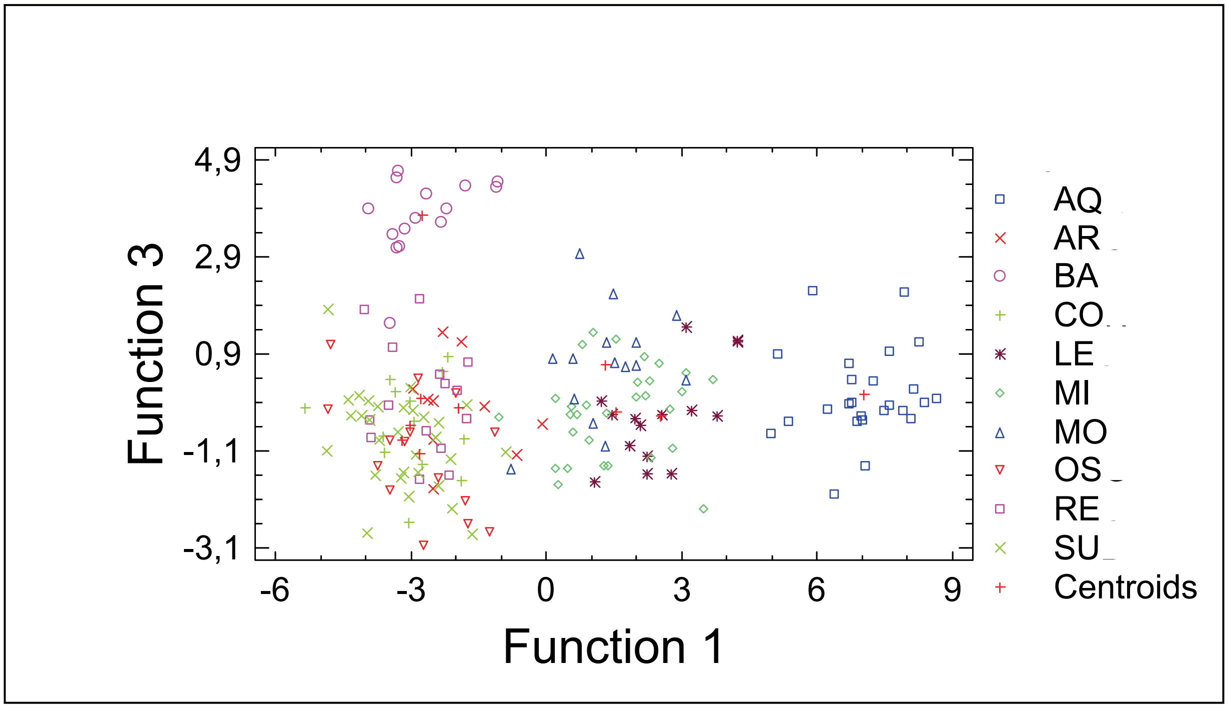


Figure 9. Plot of discriminant analysis of 183 individuals of ten taxa of the "*Momotus momota* complex" based on 14 plumage characters. **a.** Discriminant functions 1 and 2. Note the complete separation of *aequatorialis* and *lessonii* from all other taxa; the nearly complete separation of (*momota* + *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.

	Measurements				
Taxa	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

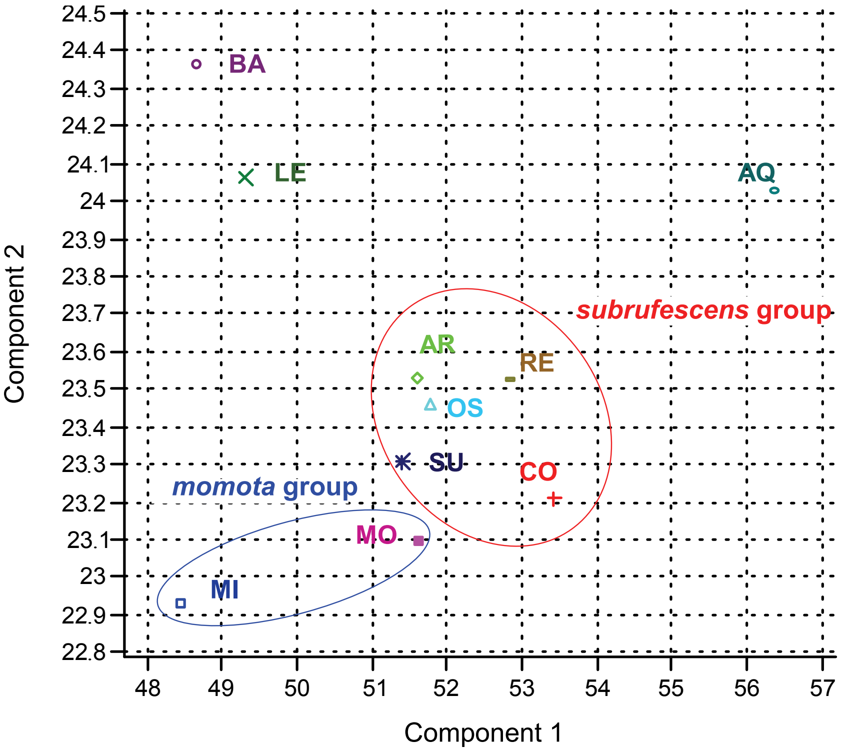


Figure 10. Principal components analysis of the relative means of five morphological measurements among ten taxa of the "*Momotus momota"* complex. Note the compact "*subrufescens* group" at center, the "*momota* group" at lower left, and the widely separated taxa *lessonii*, *aequatorialis* and especially, *bahamensis*.

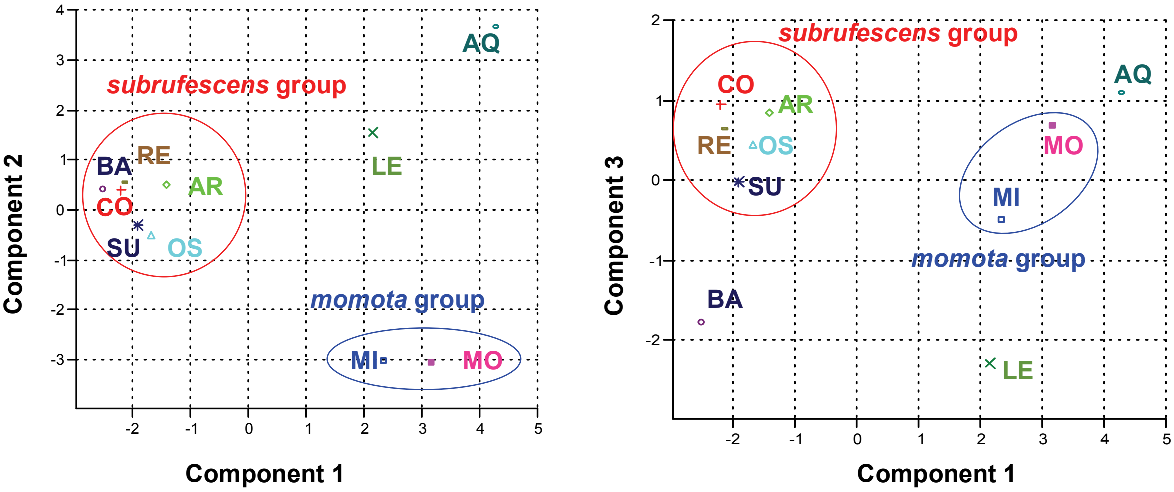


Figure 11. Principal components analysis of the relative means of five morphological characters and 14 characters of plumage pattern for ten taxa of the "*Momotus momota* complex". Note the compact clustering of the *subrufescens* group on all three components, except that *bahamensis* separtes widely 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,

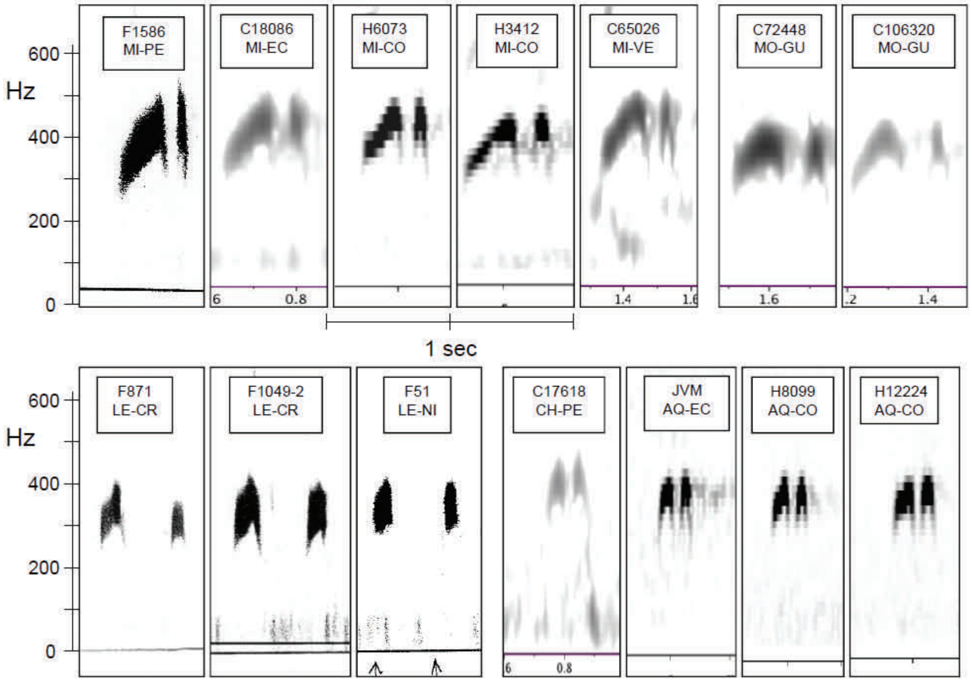


Figure 12. Sonograms of the primary songs or "hoots" of members of the "two-hoot" group of taxa. Upper left: five songs of *M. m. microstephanus* from Peru (1), Ecuador (1), Colombia (2) and Venezuela (1). Upper right: two songs of *M. m. momota* from Guyana. Lower left: two songs of *M. m. lessonii* 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.

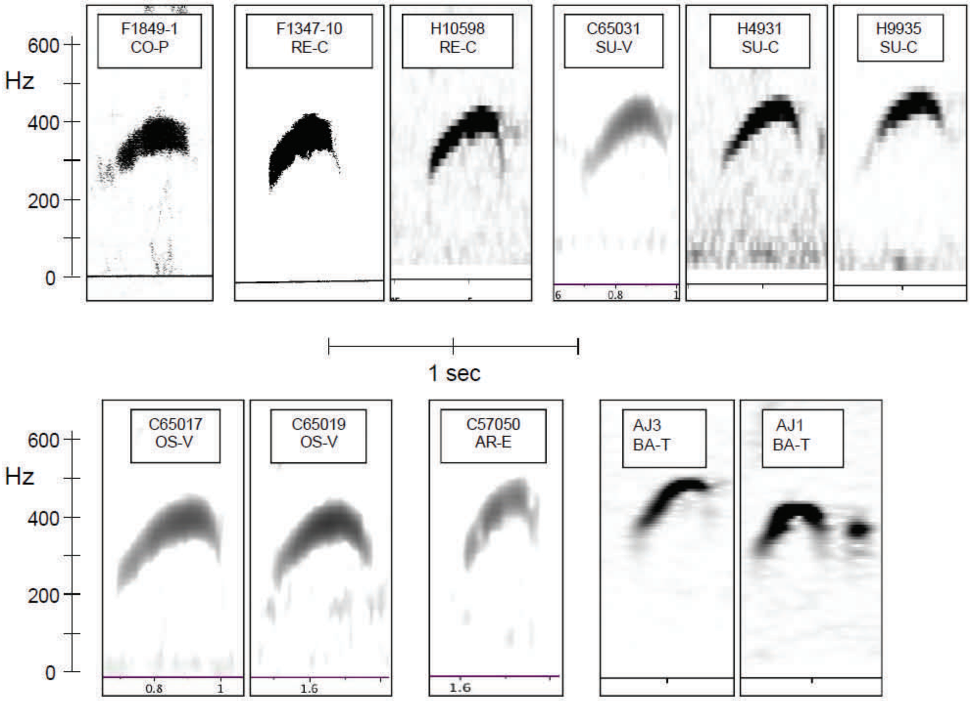


Figure 13. Sonograms of primary songs of several of the "single-hoot" taxa of the "*Momotus momota* complex". Top row, from left: one song of *conexus* from Panamá; two of *reconditus* from Colombia; one of *subrufescens* from Venezuela and two from Colombia. Bottom row: two songs of *osgoodi* from Venezuela; 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	$d_{1\text{-}2}$	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	6	181.6	124.3	0.0	0.0	0.0	362.5	479.8	456.2			
(song)		±12.3	±11.3				±28.6	±21.7	±20.3			
bahamensis	2	167.7	111.7	53.3	61.5	30.8	345.5	453.0	407.8	410.3	416.5	412.7
(duet)		±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	$d_{1\text{-}2}/d_1$	$d_{1\text{-}2}/d_2$	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	6	0.684	-	-	-	-	1.327	1.256	-	-	-
(song)		±0.025					±0,060	±0.057			
bahamensis	2	0.667	0.502	0.368	0.326	0.882	1.311	1.184	1.016	1.006	1.093
(duet)		±0.009	±0.002	±0.009	±0.082	±0.201	±0.043	±0.008	±0.006	±0.008	±0.072

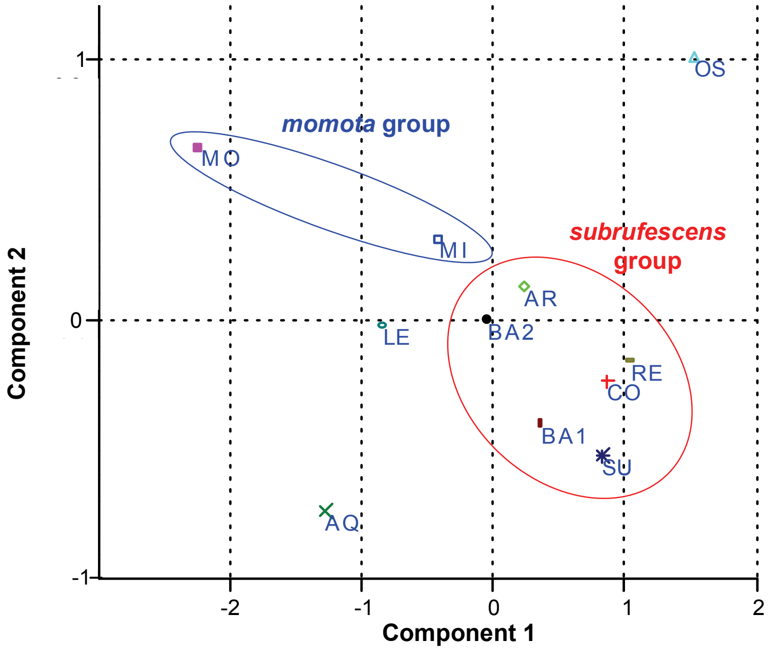


Figure 14. Principal component analysis of five parameters of the primary songs of ten taxa of the *Momotus momota* complex. Abbreviations of taxa as in Fig. 1. The single hoots of the one-note taxa are analyzed with the first hoot of the two-note taxa to determine whether these notes are similar: in 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.

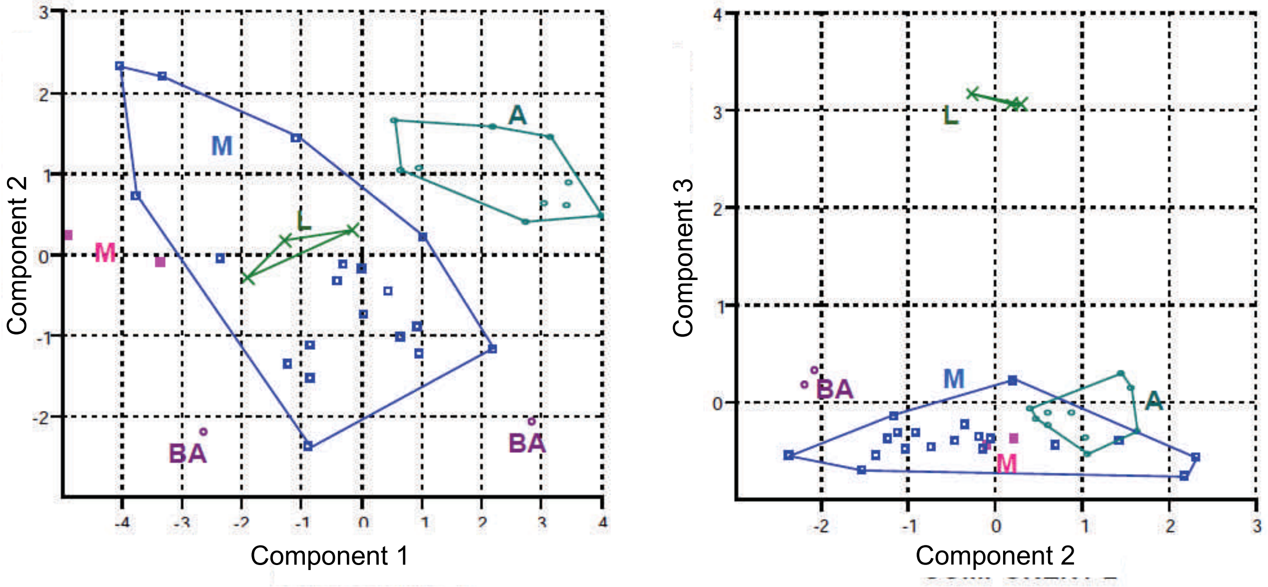


Figure 15. Principal component analysis of 11 parameters of the two-note songs of members of the *Momotus momota* complex. Included are the primary songs of *aequatorialis* (A), *lessonii* (L), *microstephanus* (M, blue) and *momota* (M, magenta) as well as the two-note duet song of *bahamensis* (BA). 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.

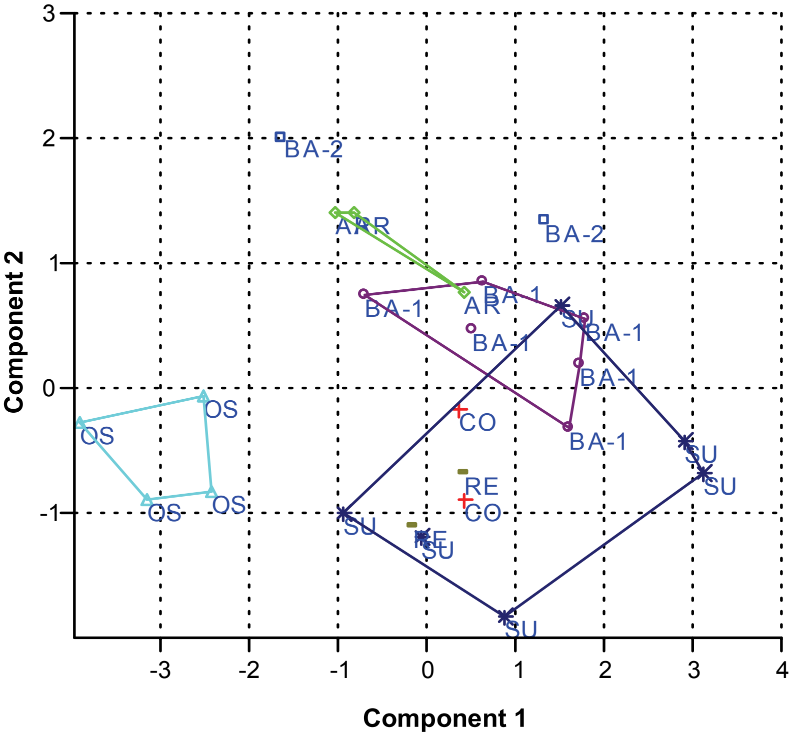


Figure 16. Principal component analysis of six characters of the single hoot of the one-note taxa of the *Momotus momota* complex. Abbreviations of taxa as in Fig. 1. BA-1 indicates the single hoot of the usual song of *bahamensis*; BA-2 indicates the first note of the song given by one member of presumed 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.

ACKNOWLEDGMENTS

Robert S. Ridgely helped me to obtain a Research Associateship at the Academy of Natural Sciences of Philadelphia that made this study possible. For access to specimens of motmots in their care, I am indebted to Leo Joseph and Nate Rice (Academy of Natural Sciences of Philadelphia); John Bates and Dave Willard (Field Museum of Natural History); Joel Cracraft and Paul Sweet (American Museum of Natural History); Mauricio Alvarez (Instituto Alexander von Humboldt, Villa de Leyva); Hno. Roque Casallas (Museo de Historia Natural, Universidad de La Salle, Bogotá) and Gilbert Barrantes (Museo de Zoología, Universidad de Costa Rica). In addition, Kristof Zyskowski measured several specimens for me in the Peabody Museum of Yale University, and I thank Gary Graves for permitting Claudia Rodríguez to measure specimens in the United States National Museum. I thank John Bates for checking plumage characters in some specimens in the Field Museum of Natural History. Mary Hennen (Field Museum of Natural History) and Nate Rice (Academy of Natural Sciences of Philadelphia) kindly photographed a number of specimens for me. For a recent opportunity to examine and measure specimens of *M. m. pilcomajensis* at the Museo de Ciencias "Bernardino Ribadavia" in Buenos Aires, I thank Julián Vedoz and Pablo Tubaro. Data on body masses of motmots were supplied by María Isabel Moreno of the Fundación ProAves of Bogotá, Miguel Lentino and Robin Restall of the Colección Ornitológica Phelps (Caracas, Venezuela), James R. Karr and Margarita Ríos.

I am greatly indebted to Jack W. Bradbury of the Macaulay Natural Sound Archives of Cornell University and Tom Webber of the University of Florida for recordings and sonograms of motmot vocalizations. Mauricio Alvarez permitted access to the natural sounds archives of the Instituto Alexander von Humboldt and other recordings were provided by John V. Moore, Alvaro Jaramillo, Eugene S. Morton and Karl S. Berg, from which Oscar Laverde kindly prepared and measured many sonograms. Field work in connection with this study was made possible by the Instituto de Ciencias Naturales of the Universidad Nacional de Colombia, and I thank the many students and colleagues there for help and companionship in the field. Earlier field work in Costa Rica had been supported by the Universidad de Costa Rica and the American Museum of Natural History; I thank Joel Cracraft and Francois Vuilleumier of this museum for a Frank M. Chapman grant to fund much of the museum work for this study.

Finally, I am grateful to Chris Witt for permission to quote from his unpublished Ph.D. thesis at the Louisiana State University, which has greatly clarified the historical biogeography of *Momotus* and several other groups of Neotropical nonpasserines, and to J. Van Remsen, Mark W. Robbins, C. Daniel Cadena and an anonymous reviewer for helpful comments on the manuscript.

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Recibido: 29 julio 2008
Aceptado 20 marzo 2009

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 Katìos	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:Filadelfia: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 Cabal:Pque.Mpal.Campoalegre	2380	S. Córdoba	1
″	H15364	Colombia:Risaralda:Sta. Rosa de Cabal: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

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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

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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

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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.

	Color of chest in relation to that of lower breast-abdomen:						
Subspecies	conspicuously greener (1)	slightly greener (2)	approximately concolor (3)	slightly more ochraceous (4)	conspicuously more ochre (5)	**N**	**Mean score**
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).

			Measurements (mm)					
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).

			Measurements (mm)					
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								
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,WAndes-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).

			Measurements (mm)					
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

Notas Breves

A SIGNIFICANT NORTHWARD RANGE EXTENSION OF MUNCHIQUE WOOD-WREN (*HENICORHINA NEGRETI*) IN THE WESTERN ANDES OF COLOMBIA

Una extensión significativa de la distribución del Cucarachero de Munchique (*Henicorhina negreti*) hacia el norte en la Cordillera Occidental de Colombia

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ABSTRACT

Henicorhina negreti is reported from the the Department of Antioquia in the Western Andes of Colombia, 350 km north of the type-locality. This finding implies that the species is much more widespread than previously thought, and calls for a re-examination of its conservation status.

Key words: *Henicorhina negreti*, range extension, conservation status.

RESUMEN

Se documenta la presencia de *Henicorhina negreti* en el Departamento de Antioquia, en la Cordillera Occidental de los Andes de Colombia, 350 km al norte de la localidad típica. Este hallazgo implica que la especie está mucho más ampliamente distribuida que lo que se pensaba, y sugiere la necesidad de volver a examinar su estado de conservación.

Palabras clave: *Henicorhina negreti*, extensión de distribución, estado de conservación.

The Munchique Wood-Wren (*Henicorhina negreti*, Troglodytidae) was described recently by Salaman *et al.* (2003), who believed it to be confined to a small part of Munchique National Park, depto. Cauca, Colombia, and considered it to be "Critically Endangered". The species was later found further north, near El Cairo (*ca*. 4°45'N, 76° 14'W), in the border between Valle del Cauca and Chocó (van Oosten & Cortes 2009), indicating that the distribution range of the species is more extensive than originally thought. Moreover, Southern Antioquia was included in the range of *H. negreti* by Kroodsma & Brewer (2005), but no reference to the source of this information was given; the present note provides the basis for this inclusion.

During field work conducted in August 2004 above Finca Primavera at a locality called La Mesenia, above the municipality of Jardín, Antioquia, near the borders of Antioquia, Caldas, Risaralda, and Chocó departments in the western slope of the Western Andes of Colombia (5°29'N, 75°54'W), I noticed that wood-wrens on the upper parts of the slope sang differently from birds lower on the slope. Playback of both song types induced birds to approach, so they could be observed at very close range. They differed distinctly from each other: the high-elevation birds exhibited darker crown, breast and flanks, more distinctly streaked throat and breast, and distinctly narrower supercilium than lower-elevation birds. These differences are in accordance with the described differences between

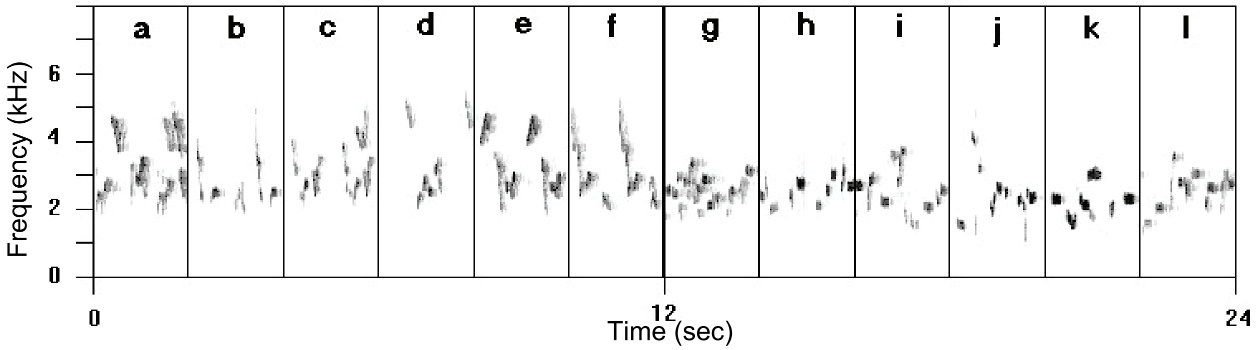

Figure 1. Extracts (2 s long) of songs of six *Henicorhina leucophrys* (a-f) and six *H. negreti* (g-l) from the Cordillera Occidental of the Andes, Colombia. Note the many long and relatively constantly pitched notes and the lack of high-pitched elements in songs of *H. negreti*. a-c: Páramo de Frontino, Antioquia, 3150 m (a), and 2600 m (b-c); d-i: above Finca Primavera, La Mesenia, Antioquia/Risaralda, 2250 m (d-f), 2300 m (g), and 2400 m (h-i); j: NW of Popayán, Cauca, 2400 m; k: Parque Nacional Munchique, Cauca, 2250 m; l: near El Cairo, Valle del Cauca/Chocó, 2200 m. Cuts a-i by N. Krabbe recorded in August 2004, j: by N. Athanas recorded in March 2005, k by P. Salaman recorded in July 2001, l by H. van Oosten recorded in February 2008.

Grey-breasted Wood-wren (*Henicorhina leucophrys*) and *H. negreti* (Salaman *et al.* 2003).

My recordings of songs of the high-elevation birds at La Mesenia were compared with recordings of *H. negreti* deposited at Xeno-Canto (XC 5147, 5148, 10651 and 18307) and were found to match them, most noticeably by being melodic, by having many long and pure notes varying little in pitch, and by lacking high-pitched elements (Fig. 1). Salaman *et al.* (2003) reported from the type locality of *H. negreti* that the two *Henicorhina* species did not respond to each others' song. On one occasion at La Mesenia, however, two family groups, one of each species, were seen to interact directly, getting within one or two meters of each other while singing loudly and giving frequent alarm calls.

Both species were encountered at the pass between Antioquia and Risaralda departments (2300 m), but *H. leucophrys* was rare on the wetter Risaralda side, *H. negreti* rare on the drier Antioquia side. At higher elevations than the pass, on the ridge itself, only *H. negreti* was encountered (to at least 2400 m). I did not venture below 2200 m on the Risaralda slope to establish whether *leucophrys* reappeared at lower elevations there.

The presence of *H. negreti* 350 km north of its type locality has important implications for conservation. Evidently, the species is much more widespread in the Western Andes than hitherto thought. Nearly all wood-wrens (including *H. negreti* above Mesenia) occur at high densities, often in highly fragmented and disturbed habitat, and large areas in the elevational range of *H. negreti* between the type locality and Mesenia, as well as further north in Antioquia remain forested (Google Earth, July 2008). I therefore suggest that the species' conservation status as 'Critically Endangered' needs to be reevaluated. A detailed mapping of wet Pacific forest at appropriate elevations, an estimate of the rate of deforestation, and field work to establish the species' presence in highly fragmented forest and to determine its true elevational range would be needed in order to accurately assess its status.

I thank Gustavo Suárez, Pablo Flórez and José Castaño for companionship during the field work.

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Recibido: 6 agosto 2008
Aceptado: 11 febrero 2009

UNA NUEVA LOCALIDAD PARA EL CUCARACHERO DE PANTANO (*CISTOTHORUS APOLINARI:* TROGLODYTIDAE) EN SOGAMOSO, BOYACÁ

A new locality for Apolinar's Wren (*Cistothorus apolinari:* Troglodytidae) in Sogamoso, Boyacá

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RESUMEN

El Cucarachero de Pantano (Troglodytidae, *Cistothorus apolinari*) es una especie amenazada y endémica de la Cordillera Oriental de Colombia, que presenta dos subespecies separadas por elevación y hábitat. Una de estas formas (*C. a. hernandezi*) habita ambientes de páramo y se conocía sólo de dos localidades distantes, los páramos de Sumapaz y El Cocuy. Aquí documentamos la existencia de una población en el Páramo de Siscunsí, Sogamoso, Boyacá, un área intermedia entre las localidades previamente conocidas. Además, presentamos información sobre la ecología y conservación de la especie en el área.

Palabras clave: Boyacá, *Cistothorus apolinari*, conservación, distribución, Páramo de Siscunsí.

ABSTRACT

Apolinar's Wren (Troglodytidae, *Cistothorus apolinari*) is an endangered species endemic to the Cordillera Oriental of Colombia comprising two subspecies that are separated by elevation and habitat. One of these forms (*C. a. hernandezi*) occurs in páramo habitats and was known only from two distant localities, Sumapaz and El Cocuy. We here document the existence of a population in the Páramo de Siscunsí, Sogamoso, Boyacá, an area between the two previously known localities. In addition, we present information on the ecology and conservation of the species in the area.

Key words: Boyacá, *Cistothorus apolinari*, conservation, distribution, Páramo de Siscunsí.

El Cucarachero de Pantano (*Cistothorus apolinari,* Troglodytidae) es una especie endémica del norte de la Cordillera Oriental de los Andes colombianos. Habita elevaciones de 2500 a 4000 m en el valle de Ubaté, la sabana de Bogotá y el páramo de Sumapaz en Cundinamarca, y la Sierra Nevada del Cocuy y el lago de Tota en Boyacá (Hilty & Brown 1986, Asociación Bogotana de Ornitología 2000, Morales-Rozo & De La Zerda 2004; Fig. 1). Existen dos subespecies de *C. apolinari* morfológicamente diferenciadas y aparentemente segregadas también por hábitat: *C. a. apolinari* habita en los humedales del altiplano cundiboyacense y *C. a. hernandezi* en los bofedales de los páramos con vegetación dominada por *Diplostephium revolutum, Chusquea tessellata* y algunas especies de *Hypericum.* Debido a la destrucción de su hábitat, *C. apolinari* es una especie amenazada de extinción (Caycedo & Renjifo 2002), por lo que el hallazgo de nuevas poblaciones es de interés particular para la conservación.

En este trabajo, documentamos la presencia del cucarachero de pantano en el Páramo de Siscunsí, Sogamoso, Boyacá, una nueva localidad para la

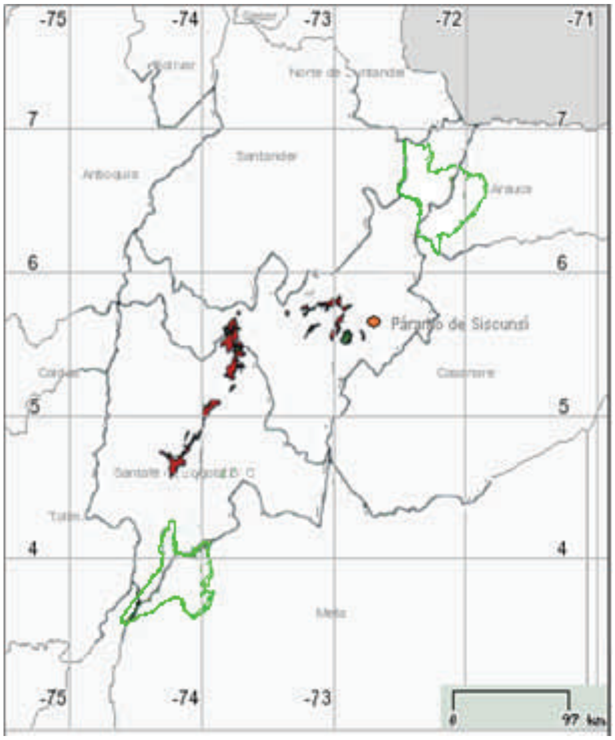

Figura 1. Distribución conocida de *Cistothorus apolinari* en la Cordillera Oriental de Colombia y ubicación del Páramo de Siscunsí, Sogamoso, Boyacá, en donde la especie fue encontrada en este estudio (área naranja). En verde claro se muestra la distribución conocida de *C. a. hernandezi,* con el Páramo de Sumapaz al suroccidente y la Sierra Nevada del Cocuy al nororiente. En rojo se muestra la distribución de *C. a. apolinari.* Mapa tomado y modificado de Caycedo & Renjifo (2002).

especie, situada en una posición geográfica intermedia entre las dos localidades de páramo hasta ahora conocidas (Stiles & Caycedo 2002). Además, presentamos información sobre la ecología, historia natural, amenazas y conservación de la especie en esta localidad.

El Páramo de Siscunsí está ubicado en la vertiente oriental de la Cordillera Oriental en los municipios de Sogamoso, Aquitania, Mongua y Monguí, departamento de Boyacá (5°35'N, 72°49'W; Fig. 1). Este páramo tiene una extensión de 13050 ha y su elevación varía entre los 3200 y 3850 m (Llano 2006). Las asociaciones vegetales dominantes son frailejonales de *Espeletia congestiflora* y *E. lopezii*, chusquedales (*Chusquea tessellata*), pequeños parches de árboles de baja altura de *Diplostephium revolutum*, pajonales de *Calamagrostis effusa*, pastizales de *Agrostis* sp. y cultivos. Además, se encuentran bofedales, lagunas de alta montaña y pendientes rocosas pronunciadas.

En tres visitas realizadas entre noviembre de 2005 y julio de 2006 al Páramo de Siscunsí, hicimos observaciones con binoculares 7x35 y 10x50 y registros auditivos a lo largo de un transecto de 1500 m de longitud, completando un total de 105 h de observación/persona. Además, hicimos muestreos con redes de niebla (12 x 2.6 m, ojo de malla 30 mm) en los bordes de la Laguna de Siscunsí, cerca de la Quebrada Iglesias y en bofedales con predominio de chusque y frailejones.

Registramos la presencia de tres grupos de *C. apolinari* conformados por un promedio de 8.3 individuos, para un total de aproximado de 25 individuos a lo largo del transecto muestreado. Las aves registradas se encontraban vocalizando y forrajeando entre la vegetación dominada por *Diplostephium revolutum, Chusquea tessellata, Hypericum lycopodioides, H. laracifolium* y *Espeletia lopezii* (Fig. 2). Nuestras observaciones del hábitat ocupado por la especie en Siscunsí concuerdan con las hechas por Caycedo (2001) en el Páramo de Sumapaz. Tras coleccionar un ejemplar adulto que depositamos en la colección del Instituto de Ciencias Naturales (ICN) de la Universidad Nacional de Colombia (Fig. 3), pudimos confirmar con base en el plumaje y medidas morfométricas que la población del Páramo de Siscunsí corresponde a la subespecie

Figura 2. Hábitat de *Cistothorus apolinari hernandezi* en el Páramo de Siscunsí.

Figura 3. Individuo macho de *Cistothorus apolinari hernandezi* capturado en el Páramo de Siscunsí.

C. a. hernandezi. Las medidas del ejemplar de Siscunsí son similares a las del holotipo de esta subespecie descrito por Stiles & Caycedo (2002).

En un área de aproximadamente 90 m^2 con predominio de *C. tessellata* y musgos del genero *Sphagnum* en los alrededores de la Laguna de Siscunsí, encontramos 11 nidos de *C. apolinari* (Fig. 4). Los nidos estaban ubicados en lugares con vegetación densa de 1-2 m de altura, muy cerca (c. 3 m) de cuerpos de agua. La anidación en este tipo de microhábitats podría servir como protección ante depredadores o inundaciones (Morales-Rozo 2005). Por lo general, los nidos se ubicaban en el centro de arbustos de *C. tessellata,* a una altura (promedio ± desviación estándar) de 93.2 ± 29.1 cm, similar a lo descrito para el Páramo de Sumapaz (Caycedo 2001). Los nidos estaban construidos con material seco de *C. tessellata* y *Calamagrostis* sp.*,* con un recubrimiento interno de hojas tomentosas de frailejón. Los nidos tenían forma globular-ovalada, con una entrada lateral dirigida hacia el centro de las macollas de chusque, similar a lo encontrado por Caycedo (2001) y Morales-Rozo (2005). Uno de los nidos (Fig. 4) medía 29 x 25 cm, 14 cm de alto externamente y su cámara interna 17 x 9 cm.

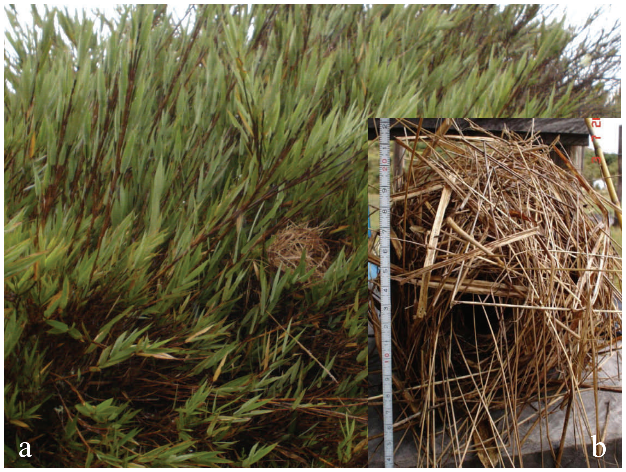

Figura 4. Nido de *Cistothorus apolinari hernandezi* encontrado en el Páramo de Siscunsí **a.** Ubicación en un parche de *Chusquea tessellata*. **b.** Vista frontal mostrando los materiales de construcción que incluían hojas de *Chusquea tessellata* y *Calamagrostis* sp. y adentro, material tomentoso de hojas de *Espeletia* sp.

El hallazgo de una población de *C. apolinari* en el Páramo de Siscunsí supone una ampliación de la distribución geográfica conocida de esta especie amenazada y representa una nueva oportunidad en cuanto a su conservación. La presencia de *C. a. hernandezi* en Siscunsí sugiere que esta subespecie podría estar distribuida de forma más continua en el corredor de páramos de la Cordillera Oriental, encontrándose en áreas entre los páramos de Sumapaz, Siscunsí y Cocuy. Sin embargo, los páramos de la Cordillera Oriental colombiana, incluyendo el de Siscunsí, están fragmentados y deteriorados como consecuencia de la expansión de áreas de pastoreo y cultivos, así como por quemas y urbanización (Mora-Osejo & Sturm 1994). Sólo una parte del Páramo de Siscunsí se encuentra actualmente delimitada como área natural protegida, la "Reserva Municipal de Siscunsí", con una extensión de 5887 ha en el municipio de Sogamoso (Llano 2006). Para garantizar la conservación de *C. apolinari* en la región, sería importante ampliar el área protegida, priorizando la inclusión de hábitats característicos para la presencia de la especie como lagunas y bofedales, los cuales actualmente carecen de protección. Una expansión del área protegida del páramo para abarcar las 7163 ha restantes (en los municipios de Aquitania, Mongua y Monguí; Fig. 5) sería recomendable, pues aunque estas zonas están intervenidas, es posible que provean hábitat propicio para la especie. De cualquier manera, es

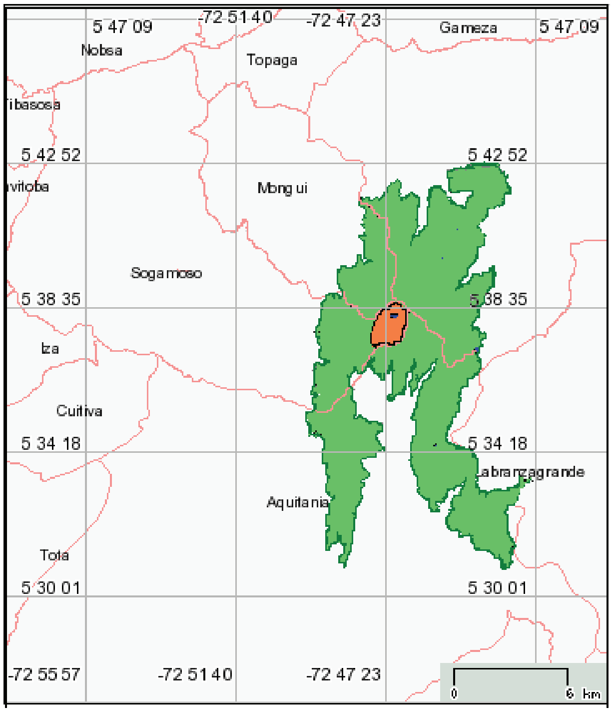

Figura 5. Área propuesta para la conservación del hábitat de *Cistothorus apolinari hernandezi* en los ambientes de páramo de los municipios de Aquitania, Sogamoso, Mongua y Monguí (en verde). El área en naranja es la extensión actual de la Reserva Municipal de Siscunsí.

importante continuar evaluando el estado actual de la población de *C. apolinari* en la región e identificar las amenazas a las que se enfrentan las poblaciones de *C. a. hernandezi* en general, que seguramente son diferentes a las que se enfrentan las poblaciones de los humedales del altiplano (Caycedo & Renjifo 2002, Cadena 2003).

Agradecemos a Andrés Cuervo, Gary Stiles y Paula Caycedo por la revisión del manuscrito, a Fausto Sáenz-Jiménez por la elaboración de los mapas, y a los integrantes del semillero de investigación del Grupo de Estudios Ornitológicos de la Universidad Pedagógica y Tecnológica de Colombia (Tunja) por su colaboración en las salidas de campo. Finalmente, damos gracias a los habitantes de la vereda Las Cañas del municipio de Sogamoso, quienes facilitaron el desarrollo de esta investigación.

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Recibido: 28 abril 2007
Aceptado: 20 febrero 2009

THE NEST, EGGS, AND NESTLINGS OF THE RUFOUS-NAPED BRUSH-FINCH (*ATLAPETES LATINUCHUS LATINUCHUS*) IN SOUTHEASTERN ECUADOR

El nido, huevos, y pichones del Matorralero Nuquirrufo (*Atlapetes latinuchus latinuchus*) en el sureste de Ecuador

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ABSTRACT

I describe observations at two nests of the Rufous-naped Brush-Finch (*Atlapetes latinuchus*) from the eastern Andes of southern Ecuador. Due largely to confusion in taxonomy and recent shifts in taxonomic affinities within the group, there has been some confusion as to nest descriptions for this widely distributed Andean genus. Although the eggs of this species have been previously described, this is the first time that the nest of the nominate subspecies has been described. Two nests of *A. l. latinuchus* were open cups similar to those of other species of *Atlapetes*; both were built near the ground in areas of disturbance. One nest took around 9 days to build, and at one nest the incubation period was 16 days and nestlings fledged after 15 days.

Key words: *Atlapetes l. latinuchus*, building, eggs, incubation, nest, nestlings, Rufous-naped Brush-Finch.

RESUMEN

Presento observaciones sobre dos nidos del Matorralero Nuquirufo (*Atlapetes latinuchus*) del este de los Andes en el sur de Ecuador. Por cambios y confusión en la taxonomía de este género con distribución amplia, ha existido confusión sobre las descripciones de sus nidos. Los huevos de *A. latinuchus* fueron descritos antes, pero aún no hay descripción del nido de la subespecie nominal. Los dos nidos de *A. l. latinuchus* encontrados eran una tazas parecidas a otros nidos del genero *Atlapetes*. Ambos fueron construidos cerca del suelo en áreas de vegetación secundaria. Para un nido, el período de construcción duró 9 días y en un nido la incubación duró 16 días y los pichones volaron después de 15 días.

Palabras clave: *Atlapetes l. latinuchus*, construcción, huevos, incubación, nido, pichones, Matorralero Nuquirrufo.

The Rufous-naped Brush-Finch (*Atlapetes latinuchus*; Figure 1) was formerly considered a subspecies of *A. rufinucha* (previously Rufous-naped Brush-Finch, now Bolivian Brush-Finch), but has recently been elevated to species status and, as it is currently defined, includes nine subspecies distributed from northern Colombia and Venezuela to northern Peru (García-Moreno & Fjeldså 1999). García-Moreno & Fjeldså (1999), however, admit that subspecies at the northern end of the range might deserve species status upon closer examination. Because of these recent taxonomic shifts in such a widely distributed species, as well as confusion over intra-generic relationships (Remsen & Graves 1995), there is some confusion in the literature over descriptions of the nest and eggs of this species group. Here I describe the nest, eggs, and nestlings of the Rufous-naped Brush-

Finch (*A. l. latinuchus*) from two nests found at the Tapichalaca Biological Reserve (04º30'S, 79º10'W), located north of Valladolid in the southeastern Zamora-Chinchipe Province of Ecuador. I also provide a summary of past nest and egg descriptions for this species, and novel information on nest building, incubation and nestling periods, mass-loss of the eggs, and growth of the nestlings.

FROM THE LITERATURE.- The first reliable information for this species comes from Sclater & Salvin (1879), who describe and illustrate the eggs of *A. latinuchus elaeoprorus* (as *Buarremon elaeoprorus*) based on material obtained in Antioquia, Colombia. This description has often been repeated for *A. rufinucha* (*sensu lato*) (*e.g.,* Armani 1985, Hilty & Brown 1986), although the wording is often modified, presumably based on the figure in Sclater & Salvin (1879). Schönwetter (1981) gives egg sizes of *A. latinuchus elaeoprorus* from Antioquia (23.4-24.1 by 16.8-17.8 mm, egg mass 3.80 g, n = 4) and size from a single egg of *A. l. latinuchus* from southeastern Ecuador or north-eastern Peru (23.0 by 17.0 mm, 3.50 g). Armani (1985) provides a description of the nest and eggs of *A. rufinucha* (*sensu lato*), but no geographic information or citation is included and it is impossible to determine to which race this description pertains. Additionally, information provided by Armani (1985) is often unreliable (K. Zyskowski pers. comm.). In short, the eggs of *A. latinuchus* have been reliably described (ssp. *elaeoprorus*), but there is no reliable description of the nest for this taxon as currently defined.

CHRONOLOGY OF OBSERVATIONS.- At 06:45 (EST) on 15 October 2004, I observed an adult Rufous-naped Brush-Finch carrying strips of dried grass into a dense clump of vegetation. I found the nest to be just beginning construction upon inspection, at that time consisting of only six 10-20 cm strips of dried grass and bromeliad leaves. These materials were laid down in a roughly criss-cross pattern, already bent upwards at the edges to begin forming a cup. Two other adults were present while one adult built, but I only observed one adult participate in building or approaching the nest site. The building adult brought material from 2-30 m away. By 19 October the nest appeared finished, and I saw no further activity at the nest until 24 October at 10:00, when I found a single egg. The nest was empty at 18:00 the previous day, and I suspect the egg was likely laid that morning. The second and final egg was laid in the morning of 25 October. Both eggs hatched in the early morning (05:00-06:00) of 10 November, giving an incubation period of 16 days. Both nestlings left the nest on the morning of 25 November, resulting in a nestling period of 15 days. The second nest was found at 07:45 on 9 August 2005, at which time an adult was flushed and I discovered two eggs. I could detect no embryonic development in either when I held them up to a strong light source.

NESTS.- The first nest was located in an open grassy area of heavy human disturbance and high traffic, only 20 m from the Tapichalaca lodging facilities. It was placed 35 cm above the ground, supported by upright stems of *Cyperus* sp. (Cyperaceae), *Equisetum* sp. (Equisetaceae), and several fern species. The structure was not woven or attached in any way to supporting structures, but rested loosely upon them. The nest itself was an untidy, open cup (low cup/base following Simon & Pacheco 2005) composed of dead and dry leaves and leaf strips from various grasses, *Cyperus* sp., bromeliads, and *Chusquea* bamboo (Fig. 1). It had a neat inner lining of finer pale fibers, mostly thin grass stems (Fig. 2). It was well hidden amongst the foliage of the supporting plants, but only

Figure 1. Adult Rufous-naped Brush-Finch brooding two 4-day-old nestlings at the Tapichalaca Biological Reserve, 14 November 2004.

Figure 2. Nest of Rufous-naped Brush-Finch with completed clutch at the Tapichalaca Biological Reserve, 9 August 2005.

slightly covered from above. Measurements were: outside diameter 15-18 cm, outside height 12 cm, inner cup diameter 6 cm, inner cup depth 6 cm. The second nest was also in an area of heavy disturbance, 3 m from a well-traveled trail through 7-10 year old second growth that is still occasionally grazed by horses. It was situated 20 cm above the ground, supported by multiple stems and blades of various grasses and sedges. It measured 14 cm wide by 9 cm tall outside, with an inner cup 6 cm in diameter and 5.5 cm deep. It was constructed in a nearly identical manner to the first nest.

EGGS.- Eggs were subelliptical, white with red-brown (and to a lesser extent pale lavender) flecking and spotting (Fig. 2). In both eggs at the first nest, and one at the second, markings were heaviest at the larger end and formed an indistinct wreath. The fourth egg (second nest) showed no distinct wreath, but showed stronger markings at the larger end. Egg characteristics are given in Table 1. I measured eggs at both nests, to the nearest 0.001 g several times during incubation, and calculated the daily percent mass-loss based on their original weights.

NESTLINGS.- At hatching, nestling skin was dark orange, and they were sparsely covered with patches of grey down on the head, back, and wings. Their gapes were bright yellow, with a dark red mouth lining. By day four, the nestlings' eyes were slitted but not open and there was significant development of contour feather tracts in the ventral, spinal, and femoral regions. Contour feathers did not break their sheaths until day five. By day six (Fig. 3), the nestlings' eyes were mostly open and wing pin feathers were just beginning to break their sheaths, not becoming obviously broken until day seven. By day 10 contour feather development was significant, with only sparse tufts of down visible. Nestlings' crowns were distinctly rufous, their backs olive-brown, bellies cinnamon, with upper breast and throat tinged olive. Flight feathers were approximately one-third broken from their sheaths. I weighed the nestlings at the first nest four days after hatching and every two days subsequently until day 10. Nestling masses are given in Table 2.

Table 2. Nestling masses (g) at different ages, from 4-days -old to 10-days-old, at a single nest of Rufous-naped Brush-Finch in southeastern Ecuador.

Nestling	Day 4	Day 6	Day 8	Day 10
1	13.7	18.7	20.6	23.3
2	13.2	17.0	19.8	22.1

ADULT BEHAVIOR.- During incubation, I observed what I believe to have been only a single adult attending the nest. This observation was supported upon hatching of the eggs, when I observed two adults feeding nestlings. One adult had well worn tail feathers, which were presumably damaged

Table 1. Characteristics of four eggs from two nests of Rufous-naped Brush-Finch in southeastern Ecuador. For the two eggs marked with an asterisk, the order of laying is not known, both showed no signs of development when first weighed but appeared to have begun development by the second weighing.

Nest #	Egg #	Size (mm)	Fresh mass (g)	% daily mass-loss
1	1	23.7 x 16.8	3.65	0.62
1	2	23.3 x 16.7	3.62	0.72
2	1*	22.9 x 17.5	3.72	1.04
2	2*	24.5 x 17.2	3.91	1.00

Figure 3. Six-day-old nestlings at a nest of Rufous-naped Brush-Finch at the Tapichalaca Biological Reserve, 16 November 2004.

during incubation, whereas the other had an intact tail. Only the adult that incubated was observed to brood the nestlings. The incubating adult, presumably the female, often stood while sitting on the eggs and peered into the nest. While standing it would lean into the nest and rapidly thrust its bill in and out of the nest lining, making the entire nest vibrate. In other species, this is thought to be a form of parasite removal and may also serve to clean the nest or to roll or reposition the eggs (Haftorn 1994). During the nestling period, I observed only the adult that had incubated perform both feeding and brooding behaviors. Both adults removed or ate fecal sacs. Often while incubating and brooding, the adult would close its eyes for brief periods (5 s to 1.5 min), presumably dozing. The distance at which the adult flushed from the nest at my approach (measured during early incubation 3 times at each nest) was similar in both nests and ranged from 1 to 2 m (mean ± SD = 1.5 ± 0.4 m).

CONCLUSIONS.- Although it is impossible to determine the current taxonomic placement of the taxon for which Armani (1985) described a nest, his description includes moss as part of the external structure of the nest (p. 317). Neither nest described here included moss in any portion of the nest, nor any components that might be expected to be incidentally covered with moss when brought to the nest. Both nests were built entirely of dried material, making the nest ideally camouflaged for the disturbed habitat surrounding both nest sites. I feel, therefore, that Armani's (1985) description likely pertains to another subspecies of *A. latinuchus* or possibly to *A. rufinucha* (*sensu stricto*). The egg descriptions from this study closely match those reported earlier for this species (Sclater & Salvin 1879, Schönwetter 1981). Similarly, the nest and eggs described here are similar in general form to the nests of other *Atlapetes* (Rowley 1962, Skutch 1967, Wetmore et al. 1984, Salaman et al. 1998, Oppel et al. 2003).

I thank the Jocotoco Foundation and the staff of Tapichalaca Biological Reserve for their support, as well as Niels Krabbe, Robert Ridgely, and F. Sornoza for their help and encouragement. My studies are supported by funds provided by Matt Kaplan and John V. and the late Ruth Ann Moore through the Population Biology Foundation as well as the Maryland Ornithological Society and Field Guides Inc. I thank Kristof Zyskowski for help with literature sources, as well as C. Daniel Cadena and an anonymous reviewer for helpful corrections to this manuscript. This is publication number 177 of the Yanayacu Natural History Research Group.

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Recibido: 17 abril 2008
Aceptado: 28 marzo 2009

PRESAS DE LA LECHUZA COMÚN (*TYTO ALBA*) EN JARDÍN, ANTIOQUIA, COLOMBIA

Prey of the Barn Owl (*Tyto alba*) in Jardín, Antioquia, Colombia

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RESUMEN

Basados en el análisis de 52 egagrópilas recolectadas en noviembre de 2006, presentamos una evaluación preliminar sobre las presas de la Lechuza Común (*Tyto alba*) en Jardín, Antioquia, Colombia. Esta es la primera información disponible para una localidad altoandina en Colombia. La Lechuza Común depredó principalmente vertebrados (80.4%). Entre éstos, los pequeños roedores (36.2%), las musarañas (21.9%) y las ranas (19.1%) fueron los más importantes. Los marsupiales (2.2%), los murciélagos (0.5%) y las aves (0.5%) fueron consumidos en menor proporción. Los Hemiptera no determinados a nivel específico (15.9%) fueron los insectos más frecuentes obtenidos en la muestra.

Palabras clave: Andes, Colombia, dieta, *Tyto alba*.

ABSTRACT

Based on the analysis of 52 pellets collected in November 2006, we present a preliminary assessment of the prey taken by Barn Owl (*Tyto alba*) in Jardín, Antioquia, Colombia. This is the first information available for a high Andean locality in Colombia. Barn owl preyed mainly on vertebrates (80.4%), especially small rodents (36.2%), shrews (21.9%), and frogs (19.1%). Marsupials (2.2%), bats (0.5%) and birds (0.5%) were preyed less often. Undetermined Hemiptera (15.9%) were the most frequent insects in the sample.

Key words: Andes, Colombia, diet, *Tyto alba*.

El estudio de la ecología trófica es esencial para entender la historia natural de las especies y brinda datos útiles para su conservación. Sin embargo, la dieta de las aves rapaces nocturnas ha sido poco estudiada en Colombia (e.g. Delgado-V. & Cataño-B. 2004, Delgado-V. et al. 2005, Delgado-V. 2007, Delgado-V. & Calderón-F. 2007). Específicamente, a diferencia del gran número de publicaciones disponibles en el sur de América del Sur, especialmente en Chile y Argentina (Pardiñas & Cirignoli 2002 y las referencias allí citadas), y en menor proporción en Brasil (Scheibler & Christoff 2004, Roda 2006, Scheibler 2007), Paraguay (Teta & Contreras 2003), Perú (Ramírez et al. 2000) y Bolivia (Vargas et al. 2002), la dieta de la Lechuza Común *Tyto alba* ha sido estudiada con poco detalle en el norte de América del Sur. En Colombia, a pesar de su amplia distribución (Hilty & Brown 1986), la dieta de la especie se conoce sólo por datos preliminares obtenidos en el valle del Río Cauca, departamento de

Antioquia (Delgado-V. & Cataño-B. 2004) y en el Urabá antioqueño (Delgado-V. & Calderón-F. 2007). En esta nota presentamos la primera información de la dieta de *T. alba* en una localidad andina colombiana.

El municipio de Jardín está ubicado en la Cordillera Occidental del departamento de Antioquia. Su cabecera municipal (ca. 5°35'N 75° 49'W, 1760 m) dista 134 km de la ciudad de Medellín. Alrededor de la cabecera municipal de Jardín se encuentran pastizales, zonas de cultivo, bosques ribereños y secundarios y algunos parches reducidos de bosque primario en algunos sectores más alejados del casco urbano (e.g. vereda La Linda, 2400-2700 m).

Cincuenta y dos egagrópilas fueron recolectadas por uno de los autores (JDR) en el campanario de la iglesia del municipio, ubicada en la plaza central del pueblo, el 13 nov 2006. En el momento de la colección, tres individuos adultos de *Tyto alba* fueron observados habitando el sitio. Toda la muestra recolectada se encontraba debajo de las perchas de estos individuos. La única egagrópila medida (Fig. 1) es de tamaño grande, pero sus medidas están dentro del rango registrado para la especie (Trejo & Ojeda 2002). No tenemos un tiempo estimado de deposición de las egagrópilas pero al menos siete de ellas estaban todavía húmedas externamente en el momento de la recolección, por lo que suponemos que fueron regurgitadas durante los dos días previos.

Las egagrópilas se dejaron secar a temperatura ambiente y todos los huesos, dientes y restos quitinosos de las presas fueron extraídos manualmente de la matriz de pelo. Identificamos cada ítem alimenticio hasta la categoría taxonómica más específica que permitiera el tipo de presa y el fragmento encontrado. Para identificar los restos rescatados de las egagrópilas,

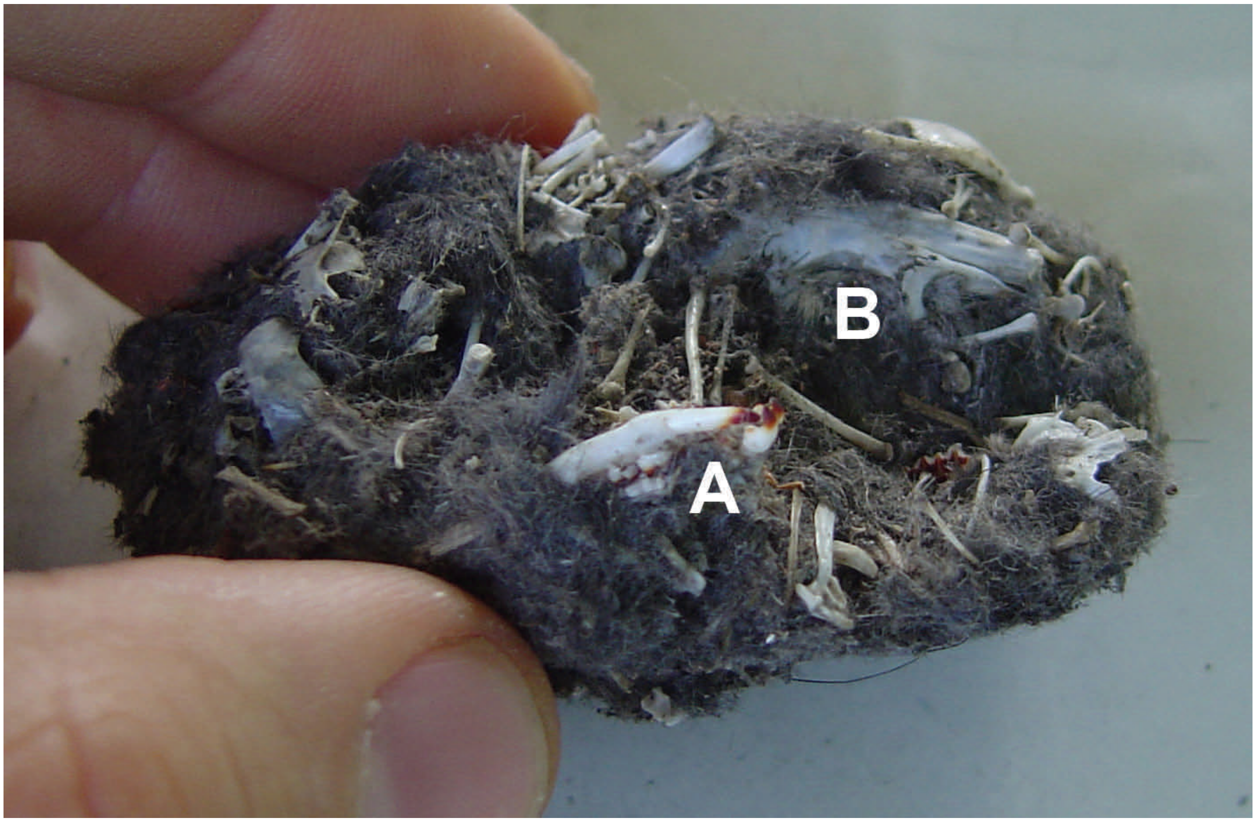

Figura 1. Una de las egagrópilas de *Tyto alba* recolectadas en Jardín, Colombia. En esta egagrópila (68 mm de largo y 36 mm de ancho), se encontraron restos de tres musarañas *Cryptotis* sp., dos ratones sigmodontinos y dos ranas. Algunas presas son detectables antes de la desintegración de la egagrópila: **A.** la mandíbula e incisivos superiores de una musaraña (note los dientes parcialmente rojos), y **B.** la parte dorsal del cráneo de un ratón sigmodontino. Otros restos parcialmente apreciables incluyen húmeros, tibias y costillas. Foto: CADV.

los comparamos con colecciones hechas previamente en el municipio que se encuentran depositadas en la Colección Teriológica de la Universidad de Antioquia CTUA. Todos los restos obtenidos de las egagrópilas fueron depositados en esta misma colección.

La importancia de cada presa en la dieta de *T. alba* en Jardín fue determinada mediante el porcentaje de presencia (número mínimo de individuos de un ítem específico dividido por el total de ítems alimenticios encontrados, multiplicado por 100; Korschgen 1980). Para evitar sobrestimación en el número de presas, en cada egagrópila tuvimos en cuenta únicamente los cráneos de los roedores (si no estaban disponibles sólo incluimos hemimandíbulas diferenciadas por lateralidad), las cinturas escapulares y los radio-ulnas de los anfibios, así como las cabezas y las mandíbulas de los insectos (Pillado & Trejo 2000).

Identificamos 183 ítems alimenticios en las muestras, entre los cuales los vertebrados (80.4%) representaron las presas más comunes. Entre éstos, los roedores (36.2%), las musarañas (21.9%) y las ranas (19.1%) conformaron el mayor porcentaje de las presas encontradas. Los insectos fueron consumidos en menor medida, pero se destaca la presencia de hemípteros de la familia Pentatomidae (15.9%). Otros vertebrados, como los marsupiales (2.2%), los murciélagos (1.9%) y las aves (1.9%) estuvieron representados en forma minoritaria (Tabla 1).

Pudimos determinar que varias especies de roedores son consumidas por *T. alba* en Jardín (Tabla 1). De hecho, esta es la localidad colombiana en donde se ha documentado la dieta más diversa en roedores hasta el momento. La predominancia de los roedores en la dieta es congruente con los resultados obtenidos en el resto de América del Sur (Pardiñas & Cirignoli 2002), incluyendo las tierras bajas de Colombia (Delgado -V. & Cataño 2004, Delgado-V. & Calderón-F. 2008).

Al analizar los resultados a un nivel taxonómico más específico, las musarañas del género *Cryptotis* (21.9%) emergen como las presas más importantes para *T. alba* en Jardín, estando presentes en las egagrópilas con una frecuencia mayor a la de cualquier especie de roedor. Aunque es probable que *Cryptotis* sea un ítem alimenticio importante para las rapaces nocturnas del norte de los Andes debido a su distribución (Woodman & Péfaur 2007) y debido a que las rapaces nocturnas frecuentemente depredan musarañas en Norte y Centro América (Colvin & McLean 1986), nuestro registro de *Cryptotis* en la dieta de *T. alba* es aparentemente sólo el segundo caso publicado de la presencia de este taxón en la dieta de una rapaz sudamericana (Araujo & Molinari 2000). Sin embargo, es de esperar que en la medida en que las investigaciones con egagrópilas aumenten, la importancia de este componente en la dieta de las rapaces nocturas, así como en otros depredadores andinos, se documente con mayor resolución.

Tabla 1. Ítems alimenticios encontrados en 52 egagrópilas de *Tyto alba* en Jardín, Colombia. N es el número mínimo de individuos por taxón.

Item	N	Porcentaje de Presencia
SORICOMORPHA		
Cryptotis sp.	40	21.9
DIDELPHIMORPHIA		
Marmosa sensu lato	4	2.2
CHIROPTERA		
Carollia sp.	1	0.5
RODENTIA		
Melanomys caliginosus	6	3.3
Handleyomys fuscatus	3	1.6
Rattus sp.	6	3.3
Akodon affinis	10	5.5
Nephelomys albigularis	6	3.3
Reithrodontomys mexicanus	2	1.1
Sigmodontinae, gen. et sp. indet. 1	29	15.9
Sigmodontinae, gen. et sp. indet. 2	4	2.2
AVES	1	0.5
ANURA	35	19.1
COLEOPTERA		
Cerambycidae	1	0.5
Dynastinae	1	0.5
Coleoptera no determinado	5	2.7
HEMIPTERA		
Pentatomidae no determinado	29	15.9

Al igual que en las zonas bajas colombianas donde *T. alba* ha sido estudiada, encontramos que los roedores sigmodontinos nativos son cazados en mayor proporción que los múridos introducidos en Jardín. Sin embargo, a diferencia de lo documentado en Porce, Antioquia (Delgado-V. & Cataño-B. 2004), en Jardín encontramos *Rattus*, y no *Mus musculus* en las egagrópilas, aunque es posible que tanto *Rattus* spp. como *M. musculus* se encuentren simultáneamente en la dieta de esta lechuza en Jardín, así como ha ocurrido en algunas localidades de Chile (Begall 2005).

Tyto alba anida en el casco urbano pero parece que no forrajea, al menos predominantemente, en éste. Con base en estimaciones del ámbito hogareño de la especie en otras localidades (ca. 7 km^2 en zonas templadas; Marti 1992) y a juzgar por la composición de las presas, es probable que *T. alba* frecuente los bosques y potreros de los alrededores de la cabecera municipal ya que los roedores nativos, las musarañas y los marsupiales que predominan en la dieta nunca han sido encontrados en el casco urbano (Delgado-V. datos no publicados). Sin embargo, las ratas introducidas (*Rattus*) presentes en la dieta de Jardín no parecen encontrarse en los bosques de las áreas rurales del municipio, lo que sugiere que algunas de las presas de *T. alba* son obtenidas en el ambiente urbano.

A diferencia de los trabajos realizados en otros ecosistemas del sur de América del Sur, donde la representación de anfibios en la dieta de *T. alba* es nula o insignificante (e.g. Bellocq 2000, Roda 2006), la representación de anfibios en la dieta de la especie en Jardín es alta. Aunque desconocemos la identidad de los anuros incluidos en la dieta en Jardín, éstos se destacan por presentar porcentajes elevados (19.1%), cercanos a los de las musarañas (21.9%). Esto concuerda con información de regiones colombianas de zonas bajas como el Urabá antioqueño, donde una rana del género *Leptodactylus* fue la presa más consumida (Delgado-V. & Calderón-F. 2007). Falta por esclarecer si esta situación es general para otras regiones del norte de América del Sur.

Nuestros datos revelan un escaso consumo de marsupiales, murciélagos y aves por parte de *T. alba* en Jardín, un resultado que es similar al obtenido en el Urabá antioqueño (Delgado-V. & Calderón-F. 2007), pero que contrasta con los de estudios realizados en Bolivia (Vargas et al. 2002), Brasil (Escarlate-Tavares & Pessôa 2005, Roda 2006) y Argentina (Noriega et al. 1993). Si bien la modificación por digestión o fractura de los mamíferos consumidos es limitada en *T. alba* (Andrews 1990), es posible que la fractura del material óseo en el caso de las aves, relacionada con sus huesos delgados y ligeros, contribuya a una subestimación de este grupo de presas en la dieta. Por esto, sería recomendable que trabajos posteriores aplicaran otras metodologías (e.g. análisis microscópico de plumas; Woodman et al. 2005), lo cual podría ayudar además a una determinación precisa de las aves depredadas (Teta & Contreras 2003).

Entre los insectos, Pentatomidae es el grupo predominante. La alta representación de estos hemípteros en la dieta de esta lechuza ya había sido documentada en Porce, Antioquia (ver Delgado-V. & Cataño-B. 2004, quienes los mencionaron como insectos no identificados). A diferencia de lo observado en Urabá, en Jardín *T. alba* no cazó cucarachas (Blattaria) ni saltamontes (Orthoptera), pero sí algunos coleópteros que contribuyen de forma mínima a su dieta (Tabla 1), así como ocurre en otras localidades de tierras bajas (Roda 2006, Delgado-V. & Calderón-F. 2007).

Aunque el número de egagrópilas analizado es bajo, es evidente que los resultados obtenidos en este trabajo, unidos a otros esfuerzos recientes realizados en Colombia (Delgado-V. & Cataño 2004, Delgado-V. & Calderón-F. 2007), permiten obtener un panorama cada vez más preciso sobre la dieta de *T. alba* en el país y el norte de América del Sur. Para continuar llenando los vacíos, motivamos a los ornitólogos y a otros investigadores a buscar egagrópilas en el campo pues éstas representan un material valioso que puede usarse para diferentes estudios, por lo que su recolección y análisis deberían considerarse seriamente por los estudiosos de la fauna en el país.

Agradecemos especialmente al encargado del mantenimiento de la iglesia del municipio de

Jardín, que permitió el acceso y la recolección de las muestras. Gracias también a Gustavo Suárez por la hospitalidad e información que siempre nos ha ofrecido en las visitas realizadas a Jardín. Agradecemos a Julio César Sáenz por la compañía y entusiasmo en las salidas de campo, y por su ayuda al recolectar las egagrópilas. Los comentarios de Ulyses F. Pardiñas y un revisor anónimo mejoraron el manuscrito.

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Recibido: 29 septiembre 2008
Aceptado: 14 abril 2009

UN NUEVO REGISTRO DEL LORO OREJIAMARILLO (*OGNORHYNCHUS ICTEROTIS*: PSITTACIDAE) EN LA CORDILLERA ORIENTAL COLOMBIANA

A New Record of the Yellow-Eared Parrot (*Ognorhynchus icterotis*: Psittacidae) in the Eastern Andes of Colombia

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RESUMEN

El Loro Orejiamarillo (*Ognorhynchus icterotis*) es una especie casi-endémica colombiana catalogada en peligro crítico (CR) según la UICN, debido especialmente a la fragmentación y perdida de su hábitat natural y a la presión de caza para alimentación. Observamos unos 30 individuos en un bosque muy húmedo premontano en el municipio de San Luis de Cubarral (Meta) asociados a la palma *Dictyocaryum lamarckianum*. Esta observación representa una extensión importante de su distribución conocida e indica que la presencia de la especie no siempre está asociada estrictamente con las palmas de cera (*Ceroxylon* spp.), lo cual tiene implicaciones para su conservación.

Palabras clave: Colombia, distribución, Cordillera Oriental, Loro orejiamarillo, *Ognorhynchus icterotis.*

ABSTRACT

The Yellow-eared Parrot (*Ognorhynchus icterotis*) is a near-endemic Colombian species catalogued as critically threatened (CR) according to the UICN, owing especially to the fragmentation and loss of its natural habitat and to subsistence hunting. We observed ca. 30 individuals in a very humid premontane forest in the municipality of San Luis de Cubarral (Meta), associated with the palm *Dictyocaryum lamarckianum*. This record represents an important extension of its currently known distribution and indicates that its presence is not strictly associated with wax palms (*Ceroxylon* spp.), which has implications for its conservation.

Key words: Colombia, distribution, Eastern Andes, *Ognorhynchus icterotis*, Yellow-eared Parrot.

El Loro Orejiamarillo (*Ognorhynchus icterotis*) es una especie casi endémica colombiana (Stiles 1998) que históricamente se distribuía en las tres cordilleras de Colombia y en el noroccidente de Ecuador (Hilty & Brown 1986), aunque actualmente se presume extinta en este último país (N. Krabbe, com. pers.). Habita los cinturones subandinos y andinos entre 2000 y 3500 m, aunque en ocasiones desciende hasta los 1200 m en bosques húmedos y áreas parcialmente deforestadas (Rodríguez-Mahecha & Hernández-Camacho 2002). En Colombia hay registros históricos en los departamentos de Antioquia, Caldas, Cauca, Huila, Nariño, Risaralda, Tolima y Norte de Santander. Este último registro, un espécimen de Ocaña de mediados del siglo XIX, fue la base de la descripción de la especie por Massena & Souance en 1854, pero aparte de esto había sólo dos avistamientos de la especie en la Cordillera Oriental: un grupo pequeño en 1975 y un individuo en 1993, ninguno de los cuales sugiere la existencia de una colonia reproductiva cercana (Rodríguez-Mahecha & Hernández-Camacho 2002, López-Lanús & Salaman 2002, Colorado et al. 2006, Cortés et al. 2006). Actualmente sólo se conocen tres poblaciones de esta especie: en Tolima en la Cordillera Central y en Antioquia y Caldas en la Cordillera Occidental (López-Lanús & Salaman 2002, Salaman et al. 2006; Fig. 1). Su reproducción supuestamente depende de la existencia de rodales de Palmas de Cera (*Ceroxylon quindiuense*) de aproximadamente 20 m de altura, donde las parejas hacen sus nidos en cavidades con entradas situadas en la parte alta o media de la palma bajo el follaje o en palmas muertas defoliadas y huecas en el ápice (Rodríguez-Mahecha & Hernández-Camacho 2002, López-Lanús & Salaman 2002). El alimento más apetecido por estos loros es el endospermo de los cocos de *Ceroxylon quindiuense* y *C. subflavescens*, aunque además consume una amplia variedad de frutos, inflorescencias y cortezas; se abastece de agua tomándola de las bromelias del género *Vriesea* (López-Lanús & Salaman 2002, Salaman et al. 2006).

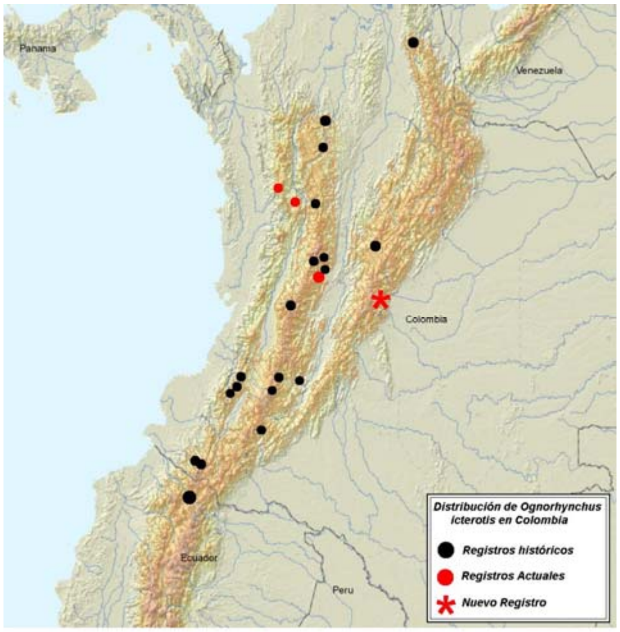

Figura 1. Distribución del Loro Orejiamarillo en Colombia: localidades de registros históricos, de poblaciones actualmente conocidas y la nueva población que registramos aquí.

La especie se considera en peligro Crítico (CR) según la UICN (2009) y en categoría B2ab (i, iv, v); C1 + 2a (i), y en el apéndice I de CITES (2009), ya que entre otros factores el 71% de su hábitat se ha perdido o ha sido degradado, y su área de reproducción conocida es sumamente pequeña (BirdLife International 2008a,b). Las acciones de conservación se dirigen principalmente a la protección efectiva de la especie por medio de la educación ambiental y la reforestación, pero se ha enfatizado la importancia de explorar áreas con registros históricos o nuevas áreas con relictos de palmar, con el fin de hallar otras poblaciones y garantizar suficientes áreas protegidas (López-Lanús & Salaman 2002, Salaman et al. 2004). Aquí informamos sobre el descubrimiento de una población más, en un bosque premontano de la ladera oriental de la Cordillera Oriental, lejos de otras localidades conocidas para la especie y no asociada con las palmas de cera sino con otro tipo de palma.

Encontramos al Loro Orejiamarillo en la parte alta del municipio de San Luis de Cubarral (3º 51´ N, 73º 53´ W), en las estribaciones de la Cordillera Oriental en el suroccidente del departamento del Meta (Fig. 1). El área de nuestras observaciones se encuentra en la zona de vida de bosque muy húmedo premontano (bmh-PM) a elevaciones entre 1650 y 1700 m, con temperaturas que oscilan entre los 12º y 23º C y precipitaciones superiores a los 4000 mm anuales. Los bosques que predominan en la región presentan buen estado de conservación, pese al aprovechamiento selectivo de especies maderables. Presentan tres estratos claramente definidos (de 3 a 18 m), con altura promedio de 15 m. Las especies dominantes de plantas leñosas incluyen a *Croizatia* cf. *neotropica, Clusia haughti, Alchornea glandulosa, Hyeronima* cf. *oblonga, Elaeagia* sp., *Aphelandra* cf. *barkleyi, Ardisia* sp., *Croton* sp., *Billia rosea y Dictyocaryum lamarckianum,* esta última conocida localmente como "palma choapo" o "barrigona" y aparentemente la especie más importante para los loros. Las familias más abundantes son Euphorbiaceae, Clusiaceae, Rubiaceae, Myrtaceae, Cunoniaceae y Myrsinaceae. (Ballesteros-Muñoz & Villate-Torres 2009; Fig. 2).

Figura 2. Vista panorámica del área de bosque montano habitada por *Ognorhynchus icterotis* en el municipio de San Luis de Cubarral, departamento del Meta. Las palmas altas son de *Dictyocaryum lamarckianum* o "palma choapo", la cual provee sitios de anidación y frutos consumidos por el loro en esta región. Foto: L. Carvajal.

Durante la fase de campo de su trabajo de grado sobre la avifauna de las veredas Vergel Alto y Palomas del municipio de San Luis de Cubarral, MAMN obtuvo información de pobladores de la zona que indicaba la presencia de *O. icterotis*; uno de ellos conservaba una cabeza disecada de este loro. Para confirmar este registro tan sorprendente, hicimos una visita a la zona entre 5 y 8 de mayo de 2009. Con base en la información suministrada por los pobladores y la observación de los movimientos de una bandada de *O. icterotis* y las vocalizaciones que realizaban al desplazarse, definimos cuatro rutas de búsqueda aprovechando senderos existentes. La primera ruta consistió en un recorrido de ca. 300 m hacia el norte del sitio de alojamiento en busca de una palma seca de choapo en la cual los pobladores habían observado una pareja de *O. icterotis* en días anteriores. Las otras rutas se extendieron ca. 2 km hacia el norte, noreste y este hacia zonas en donde los pobladores habían notado la presencia del loro y las palmas en que habitaban. Durante los recorridos registramos los números de individuos de *O. icterotis* observados y sus actividades, las plantas en donde se observaron y la posición geográfica de cada observación. También logramos registros fotográficos de *O. icterotis* y de algunos de los frutos que hacen parte de su dieta, según lo manifestado por el guía local (Fig. 3).

Figura 3. Frutos y semillas de tres especies de árboles importantes en la dieta de *Ognorhynchus icterotis* en San Luis de Cubarral. **a.** Palma choapo, *Dictyocaryum lamarckianum* (Foto: D. Beltrán); **b.** Manzano, *Billia rosea*; **c.** Palo de pollo, *Ruagea glabra* (fotos b y c tomadas de Carvajal-Rojas et al. 2008).

A nuestra llegada a la zona, escuchamos y observamos una bandada de 22 individuos de *O. icterotis* que sobrevolaban la ladera constantemente a lo largo del día, aparentemente moviéndose entre los rodales de palma choapo, lo que permitió establecer las áreas de permanencia. Este comportamiento se repitió a lo largo de nuestra estadía en el área. Al recorrer la primera ruta, encontramos una pareja en una cavidad con doble entrada en el estípite seco de una palma choapo (Fig. 4). La pareja permaneció en la cavidad por 40 minutos y luego voló hacia el este. Al siguiente día una fuerte ventisca derribó la palma, lo que nos permitió acceder al hueco en busca de rastros de anidación, pero éste estaba vacío.

Figura 4. Un individuo adulto de *Ognorhynchus icterotis* en el hueco de una palma choapo que fue derribado por el viento el día siguiente; el hueco estaba vacío. Foto: M. Murcia.

Después de recorrer aproximadamente 1 km de la segunda ruta, observamos una pareja de loros llegando desde el sur a la copa de un árbol de unos 25 m de altura. Uno de ellos buscó agua en una bromelia (*Vriesia* sp.); ambos permanecieron en el árbol durante unos diez minutos y luego volaron hacia el norte. En la mañana siguiente observamos hacia el noreste una pareja del Milano Tijereta (*Elanoides forficatus*) sobrevolando los sitios donde se hallaban los loros, a lo cual éstos reaccionaron con vocalizaciones fuertes y constantes. Por ello decidimos buscar más individuos en la dirección desde donde los escuchábamos y definimos el tercer trayecto. Allí encontramos un individuo adulto en el ápice de un estípite seco de choapo que presentaba además un hueco a unos 3 m por debajo del ápice; luego de unos minutos emergió del interior del ápice otro individuo (Fig. 5) y después de 10 minutos los dos volaron hacia el este. Finalmente, observamos un grupo de tres loros sobre el fuste de un drago (*Croton* sp.) junto a una palma choapo de aproximadamente 25 m de altura; unos minutos después el grupo voló en dirección sur.

Figura 5. Dos adultos en el ápice de un estípite seco de palma choapo. Foto: D. Beltrán.

En total obervamos unos 30 individuos de *Ognorhynchus icterotis* en esta expedición. Los moradores del lugar nos informaron que la población de loros se ha mantenido en la zona por lo menos desde 1962 cuando llegaron al lugar y que durante las épocas de fructificación de algunas especies de árboles, notablemente Palo de Pollo (*Ruagea glabra*), los números de loros son mucho mayores. Según sus observaciones, otras especies cuyos frutos son consumidos por el loro son Manzano (*Billia rosea*), guamos (*Inga* spp.), Yarumo (*Cecropia* sp.) y Drago (*Croton* sp.); fue en este último árbol que fue cazado el individuo cuya cabeza disecada nos alertó sobre la presencia de la especie. Con base en esta información, la población de *O. icterotis* de la zona podría ser por lo menos parcialmente migratoria o nómada siguiendo las cosechas de ciertos frutos. Un comportamiento similar ha sido registrado en otras poblaciones de la especie (Salaman et al. 2002, 2006). Puesto que el grupo GEMA del Instituto Humboldt hizo muestreos en esta vertiente de la Cordillera Oriental tanto al norte como al sur de Cubarral sin haber encontrado indicios de *O. icterotis* (Bohórquez 2002, Salaman et al. 2002), es probable que el ámbito de acción de esta población no sea muy extenso. Tomando en cuenta la gran distancia a la población del Tolima, que aunque se encuentra en la Cordillera Central es la más cercana de las conocidas en la actualidad, creemos haber encontrado una población previamente desconocida.

Este descubrimiento representa el primer registro de *O. icterotis* sobre la vertiente oriental de la Cordillera Oriental desde la descripción de la especie por Massena & Souancé (la localidad típica, Ocaña en Norte de Santander, es también la única conocida en la cuenca del Orinoco). Aunque los registros y observaciones históricas del Loro Orejiamarillo siempre han estado relacionados con rodales de palma de cera (*Ceroxylon* spp.), nuestro registro demuestra que el loro también puede usar otras palmas para su ciclo vital y resalta la importancia de conservación del área y su vegetación, en especial de la palma choapo. Esto también abre más posibilidades para buscar otras poblaciones desconocidas, especialmente en esta vertiente, ya que la búsqueda no tiene que limitarse a sitios con palmas de cera.

Recomendamos estudios más detallados en la región de Cubarral para documentar varios aspectos de la ecología de *O. icterotis* en esta región. Se debe extender el inventario de la población a las zonas circundantes para documentar las épocas y extensiones de sus movimientos estacionales, su uso de diferentes frutos y el grado de su dependencia de la palma choapo tanto para anidación como para alimentación y sus temporadas de reproducción y muda. Este registro, además de complementar sustancialmente el conocimiento de la especie, serviría como base para establecer planes de conservación de esta población tan singular de una especie muy amenazada.

AGRADECIMIENTOS

Agradecemos a CORMACARENA por la financiación de este proyecto, en especial a Beltsy G. Barrera, Eduardo Sánchez y Diana Puentes. Damos las gracias a Pedro Alirio Ruge por su acompañamiento en campo y a los pobladores de la región, especialmente Carlos Fernández, doña Sara y Gabriel Fernández, por su amabilidad y hospitalidad. Agradecemos a los profesores Jorge E. Morales S. y José E. Cely por su apoyo y amistad, al Grupo Estudiantil de Ornitología de la Universidad Distrital "Francisco José de Caldas" GEO-UD, a F. Gary Stiles, C. Daniel Cadena, Luis Miguel Renjifo y Humberto Álvarez-López por la revisión del manuscrito y a nuestros compañeros y amigos Astrid Castellanos, Camilo Díaz, Diego Quiroga y Diego Coy.

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Recibido: 7 mayo 2009
Aceptado: 15 junio 2009

Resúmenes de Tesis

Navas-Berdugo, Ángela Patricia. 2008

Filogeografía y patrones de variación de genética y morfológica en *Diglossa albilatera* (Aves: Thraupidae): Probando la influencia del aislamiento y de la evolución adaptativa en la diferenciación poblacional. 53 p. (en inglés).

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Las montañas neotropicales representan uno de los "hotspots" de endemismo, diversidad y especies amenazadas en el mundo. Tradicionalmente, el surgimiento de la gran diversidad en estas montañas ha sido explicado por la influencia de las barreras geográficas en el aislamiento de las poblaciones que se han diversificado en alopatría. Sin embargo, los gradientes altitudinales y la complejidad topográfica en las regiones de montaña llevan a la existencia de distintos ambientes a lo largo de distancias muy cortas, lo cual puede haber influenciado la diversificación de las aves de esta región como resultado de variación geográfica de las presiones selectivas. En este estudio analizo los patrones de diferenciación en *Diglossa albilatera* (Aves, Thraupidae) en Colombia y Venezuela evaluando la variación genética (ADN mitocondrial) y morfológica a lo largo de su rango de distribución y su relación con la variación ecológica (climática). Los análisis filogenéticos muestran que *D. albilatera* es una especie monofilética que comprende dos clados, uno que incluye poblaciones de los Andes colombianos y un haplotipo de la pendiente venezolana de la Serranía del Perijá, y otro que incluye poblaciones de los Andes venezolanos, ambas pendientes de la Serranía del Perijá y un subclado de la Sierra Nevada de Santa Marta. Los análisis de genética de poblaciones sugieren una diversificación reciente a lo largo de las montañas colombianas, acompañada por flujo genético entre cordilleras. Los análisis morfológicos no revelan diferencias sustanciales entre regiones y la asociación entre variación genética, morfológica y climática es débil o inexistente. Concluyo que el tiempo y aislamiento han sido insuficientes para llevar a diferenciación morfológica entre las poblaciones de *D. albilatera*. Sin embargo, debido a que si la selección es lo suficientemente fuerte la diferenciación morfológica puede ocurrir rápidamente, incluso en presencia de flujo genético, una interpretación alternativa es que las diferencias en presiones de selección en esta parte de la distribución de la especie son sutiles. Ampliar la cobertura molecular y morfológica a lo largo de toda la distribución de la especie es necesario para tener un mejor entendimiento de las fuerzas que están influenciando la diferenciación a nivel poblacional.