SHORT COMMUNICATIONS

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FURTHER EVIDENCE FOR PARAPHYLY OF THE FORMICARIIDAE (PASSERIFORMES)

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Abstract. The historical relationships of ground antbirds and their relatives have long been unresolved. Here, I present a phylogenetic analysis of ground antbird (Formicariidae) relationships based on DNA sequence data from the cytochrome-*b* and ND2 genes. Results support novel hypotheses of historical relationships, including two revisions of suboscine taxonomy: (1) paraphyly of the Formicariidae with the tentative inclusion of at least some *rhinocryptids* (*Liosceles*, *Rhinocrypta*, and *Scytalopus*) in the ground antbird lineage, and (2) placement of *Pittasoma* with *Conopophaga* in the Conopophagidae.

Key words: antthrush, Conopophaga, *phylogeny*, Pittasoma, *tapaculo.*

Evidencia Adicional sobre el Carácter Parafilético de Formicariidae (Paseriformes)

Resumen. Las relaciones históricas entre los Formicariidae y sus parientes han permanecido sin resolver por mucho tiempo. Aquí presento un análisis filogenético de las relaciones de los Formicariidae basado en datos de secuencias de ADN de los genes citocromo-*b* y ND2. Los resultados apoyan nuevas hipótesis sobre las relaciones históricas, incluyendo dos revisiones acerca de la taxonomía de los suboscines: la inclusión tentativa de al menos algunos rinocríptidos (*Liosceles*, *Rhinocrypta* y *Scytalopus*) en Formicariidae, y el emplazamiento de *Pittasoma* en Conopophagidae.

The ground antbirds (Formicariidae) form a diverse clade of suboscine passerines that currently includes six genera: *Formicarius*, *Chamaeza*, *Grallaria*, *Grallaricula*, *Myrmothera*, and *Hylopezus* (Sibley and Ahlquist 1990, Ridgely and Tudor 1994, Rice 2000, 2005). Most species are plainly colored, and, as the name implies, are typically found on or near the ground. The Formicariidae has not been the subject of any detailed phylogenetic study, with most current research focused on alpha taxonomy and natural history (Graves 1987, Stiles 1992, Kratter 1995, Krabbe et al. 1997, Barber and Robbins 2002); however, Rice (2005) does provide an overview of generic-level phylogenetic relationships of the antpittas.

Ames (1971) examined a broad diversity of antbirds and separated them into two groups (ground antbirds and typical antbirds) on the basis of their syringeal morphology. He hypothesized that ground antbird syrinxes were intermediate between those of typical antbirds and tapaculos. Sibley and Ahlquist (1990) used DNA-DNA hybridization data to identify ground antbirds as a monophyletic lineage distinct from typical antbirds. The Conopophagidae (gnateaters) and Rhinocryptidae (tapaculos) were identified as their closest relatives. However, because Sibley and Ahlquist (1990) examined only six formicariid taxa, and radioactively labeled only one, a family-wide perspective was lacking.

Two recent studies of higher-level tracheophone systematics have suggested that the Formicariidae is paraphyletic (Irestedt et al. 2002, Chesser 2004). In both studies, the antthrushes (*Chamaeza* and *Formicarius*) and antpittas (*Grallaria*, *Grallaricula*, *Hylopezus*, and *Myrmothera*) each formed monophyletic lineages, but were not each other's sister lineage. Irestedt et al. (2002) and Chesser (2004) found that the antthrushes formed the sister group to the Dendrocolaptidae and Furnariidae, and in some analyses included tapaculos as their sister group. The antpittas were the sister group to the antthrushes + Dendrocolaptidae + Furnariidae lineage. As the focus of these recent studies was at the family- and subfamily-level, they thus included very few ground antbirds (one individual each of *Formi-*

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TABLE 1. Tissue numbers, collections, and Genbank numbers of the taxa examined in this study.

Taxa	Common name	Collection[a]	Tissue number	Genbank numbers[b]
Myrmornis torquata	Wing-banded Antbird	KUMNH	1311	AY370565, AY370602
Phlegopsis nigromaculata	Black-spotted Bare-eye	KUMNH	447	AY370561, AY370598
Thamnophilus doliatus	Barred Antshrike	FMNH	1286	AY370563, AY370600
Liosceles thoracicus	Rusty-belted Tapaculo	FMNH	4545	AY370558, AY370595
Rhinocrypta lanceolata	Crested Gallito	LSUMNS	18 813	AY370559, AY370596
Scytalopus magellanicus	Andean Tapaculo	LSUMNS	8343	AY370560, AY370597
Conopophaga lineata	Rufous Gnateater	FMNH	5288	AY370555, AY370592
C. peruviana	Ash-throated Gnateater	KUMNH	672	AY370554, AY370591
Chamaeza campanisona	Short-tailed Antthrush	LSUMNS	5385	AY370536, AY370573
C. mollissima	Barred Antthrush	FMNH	1490	AY370537, AY370574
Formicarius colma	Rufous-capped Antthrush	KUMNH	775	AY370550, AY370587
F. analis	Black-faced Antthrush	KUMNH	709	AY370551, AY370588
Grallaricula lineifrons	Cresent-faced Antpitta	ANSP	3869	AY370538, AY370575
G. flavirostris	Ochre-breasted Antpitta	LSUMNS	7973	AY370539, AY370576
Myrmothera campanisona	Thrush-like Antpitta	LSUMNS	9600	AY370548, AY370585
M. simplex	Tepui Antpitta	LSUMNS	7408	AY370549, AY370586
Hylopezus fulviventris	White-lored Antpitta	ANSP	4282	AY370552, AY370589
H. berlepschi	Amazonian Antpitta	FMNH	1421	AY370553, AY370590
Grallaria squamigera	Undulated Antpitta	LSUMNS	6254	AY370540, AY370577
G. varia	Variegated Antpitta	LSUMNS	7528	AY370541, AY370578
G. rufula	Rufous Antpitta	LSUMNS	1218	AY370542, AY370579
G. blakei	Chestnut Antpitta	LSUMNS	5620	AY370543, AY370580
G. ruficapilla	Chestnut-crowned Antpitta	ANSP	4810	AY370544, AY370581
G. watkinsi	Watkins' Antpitta	ANSP	2906	AY370545, AY370582
G. eludens	Elusive Antpitta	LSUMNS	11 263	AY370546, AY370583
G. dignissima	Ochre-striped Antpitta	ANSP	3229	AY370547, AY370584
Pittasoma rufopileatum	Rufous-crowned Antpitta	LSUMNS	11 860	AY370556, AY370593
P. michleri	Black-crowned Antpitta	LSUMNS	2285	AY370557, AY370594
Procnias nudicollis	Bare-throated Bellbird	KUMNH	110	AY370571, AY370608
Rupicola rupicola	Guianan Cock-of-the-rock	LSUMNS	7575	AY370572, AY370609

[a] Collection acronyms are as follows: KUMNH = University of Kansas Natural History Museum, LSUMNS = Louisiana State University Museum of Natural Science, FMNH = Field Museum of Natural History, ANSP = Academy of Natural Sciences of Philadelphia.

[b] Genbank numbers are cytochrome-*b* and ND-2, respectively.

carius, *Chamaeza*, *Grallaria*, and *Hylopezus* [Irestedt et al. 2002], and one individual each of *Formicarius*, *Grallaria*, *Myrmothera*, and *Grallaricula* [Chesser 2004]). Here, I present additional molecular evidence for the paraphyly of the ground antbirds using improved taxon sampling from the ground antbird (18 species) and tapaculo (three species) lineages.

METHODS

TAXA EXAMINED

DNA sequences were analyzed for at least two species from each currently recognized genus of ground antbird, and eight species from *Grallaria*, accounting for nearly one-third of all ground antbird species. Representatives of four other suboscine families, four conopophagids, three rhinocryptids, three thamnophilids, and two cotingids were also sequenced, for a total of 30 species sampled (Table 1). In each case, representatives of genera or families were chosen to be as phenotypically disparate as possible. Freshly frozen or ethanol-preserved tissues (liver, heart, and muscle) were obtained from the Louisiana State University Museum of Natural Science (LSUMNS), Field Museum of Natural History (FMNH), Academy of Natural Sciences (ANSP), and University of Kansas Natural History Museum (KUNHM).

MOLECULAR METHODS

DNA extraction, amplification, and sequencing protocols follow those outlined in Rice et al. (2003) and Rice (2005). Genomic DNA was extracted from each sample using Qiamp tissue extraction kits (Qiagen, Valencia, California). The 3′ end of the cytochrome-*b* gene (378 bp) and a segment of the ND2 gene (501 bp) were amplified using conventional thermal-cycling techniques (Kocher et al. 1989). Cytochrome-*b* primers (H-15915, 5′–CCAGACCTCCTAGGAGACCCAGA–3′ and L-15507, 5′–AACTGCAGTCATCTCCGGTTTACAAGAC–3′) were developed by S. Hackett (pers. comm.), and ND-2 primers (H-6313, 5′–GGCTGAATRGGMCTNAAYCARAC–3′ and L-5757, 5′–CTCTTATTTAAGGCTTTGAAGGC–3′) were developed by M. Sorenson (pers. comm.). The thermal profile used for both primer sets was denaturing at 95°C for 30 sec, annealing at 55°C for 30 sec, and extension at 70°C for 90 sec. Extension time was lengthened 4 sec

per cycle for 35 cycles. Target DNA amplified using the thermal cycler was then purified using low-melt (1%) NuSieve GTG agarose gel (FMC BioProducts, Rockland, Maine) electrophoresis for 45 min at 85–95 volts. Bands containing target products were excised from the low-melt electrophoresis gel and the DNA was recovered using Qiaquick spin columns (Qiagen, Valencia, California). Purified product was amplified using only one primer (heavy or light) and sequenced with an ABI Prism Genetic Analyzer (Model 310, Applied Biosystems, Foster City, California). The thermal profile used for both primer systems was denaturing at 96°C for 10 sec, annealing at 50°C for 5 sec, and extension at 60°C for 4 min, repeated for 25 cycles. Negative controls were used at each step of DNA preparation to test for reagent contamination. All DNA sequences are deposited in Genbank (Table 1).

DATA ANALYSES

Separate character-state matrices were assembled for cytochrome-*b* and ND2 gene sequences. Heavy and light strands were spliced and aligned using the clustal algorithm of Sequence Navigator (ABI Prism, Foster City, California). Phylogenetic analyses were conducted for both data sets individually and combined to assess congruence of data sets. Data were analyzed using maximum parsimony and maximum likelihood optimizations, with the cotingids *Rupicola rupicola* and *Procnias nudicollis* designated as outgroups.

Parsimony analyses of the equally weighted, unordered datasets were conducted using heuristic searches with 1000 random-taxon addition replications, and the tree bisection-reconnection and steepest descent options of PAUP 4.0b10 (Swofford 2002). Although no saturation was detected in the dataset, additional analyses were performed using various weighting schemes to test the sensitivity of the results to assumptions, including a 2:1 weighting of transversions-transitions and downweighting of third position bases by factors of 2, 5, and 10. Lineage support was assessed using bootstrap values based on 1000 replications, each with 20 random taxon addition replications, and Bremer branch-support values (Bremer 1994, Sorenson 1996).

Maximum likelihood analyses were performed on the datasets using heuristic searches with 10 random addition replications in PAUP 4.0b10 (Swofford 2002). I used MODELTEST 3.0 (Posada and Crandall 1998) to assess 56 models of DNA sequence evolution and determine the model that best explained the sequences analyzed. The GTR + G + I model was found to be the most efficient at optimizing sequence evolution for this dataset, with the following parameters: prob. [A–C] = 0.29, prob. [A–G] = 13.32, prob. [A–T] = 0.46, prob. [C–G] = 0.65, prob. [C–T] = 4.81, prob. [G–T] = 1.00; freq. [A] = 0.37, freq. [C] = 0.38, freq. [G] = 0.04, freq. [T] = 0.21; shape parameter = 0.75; and proportion of invariant sites = 0.36. Support for particular clades was assessed on the maximum likelihood topology by bootstrapping using 100 heuristic searches with random addition replicates.

RESULTS

MOLECULAR RESULTS

The aligned data matrix included 879 molecular characters (378 from cytochrome-*b* and 501 from ND2); 470 (54%) of which were phylogenetically informative. Inspection of sequences did not reveal any insertions, deletions, or sequencing artifacts and sequences translated successfully into amino acids, suggesting that the sequences are mitochondrial and not nuclear pseudogenes. Mean uncorrected pairwise divergence among taxa included in this study was 21% and ranged from 5% (between the two *Myrmothera* species) to 26% (between *Liosceles* and *Pittasoma rufopileatum*). The base frequencies calculated from the dataset were: [A] = 32%, [C] = 33%, [G] = 9%, and [T] = 27%, and the transition-transversion ratio calculated from the most parsimonious tree was 1.41.

Numbers of phylogenetically informative and variable sites varied by the gene region analyzed as well as by coding position. For the cytochrome-*b* gene region, there were 193 variable sites, and 175 of these were phylogenetically informative. Partitioning by codon position revealed that first positions had 49 variable sites (42 phylogenetically informative), second positions had 21 variable sites (15 phylogenetically informative), and there were 124 variable sites for third positions (118 phylogenetically informative). For the ND2 gene region, 337 variable sites were detected, of which 295 were phylogenetically informative. Partitioning by codon position revealed that first positions displayed 105 variable sites (90 phylogenetically informative), second positions had 68 variable sites (48 phylogenetically informative), and there were 164 variable sites for third positions (157 phylogenetically informative).

PHYLOGENETIC RESULTS

Parsimony analysis of the combined molecular dataset resulted in three most parsimonious trees (Fig. 1, tree length = 2436, consistency index = 0.34, homoplasy index = 0.66, retention index = 0.44, rescaled consistency index = 0.15). The only difference among these trees was that in one tree the sister relationship between the antthrushes and tapaculos was not recognized. In another, the sister relationship between the typical antbirds and *Pittasoma* + *Conopophaga* was not recognized. In all the most parsimonious trees, the tracheophones formed a monophyletic lineage, with the tapaculos and ground antbirds (excluding *Pittasoma*) forming a monophyletic lineage. Maximum likelihood analyses of the same dataset produced a single most likely tree (Fig. 1, score = −Ln 10 767) that was topologically identical to the majority rule consensus tree.

Using two cotingid taxa as outgroups, the 28 tracheophones included in this analysis formed a well-supported monophyletic lineage of two major clades. The first clade was the sister relationship between the typical antbirds and *Pittasoma* + *Conopophaga*. The second major tracheophone lineage included the ground antbirds and tapaculos sequenced for this study, and is well supported by bootstrap replicates in both character optimization analyses.

Within this second tracheophone lineage are two subclades, the antpittas (*Grallaria*, *Grallaricula*, *Hylopezus*, and *Myrmothera*) and the antthrushes (*Chamaeza* and *Formicarius*) + tapaculos (*Liosceles*, *Rhinocrypta*, and *Scytalopus*). The antpittas form a well-supported clade of two sublineages. In one lineage,

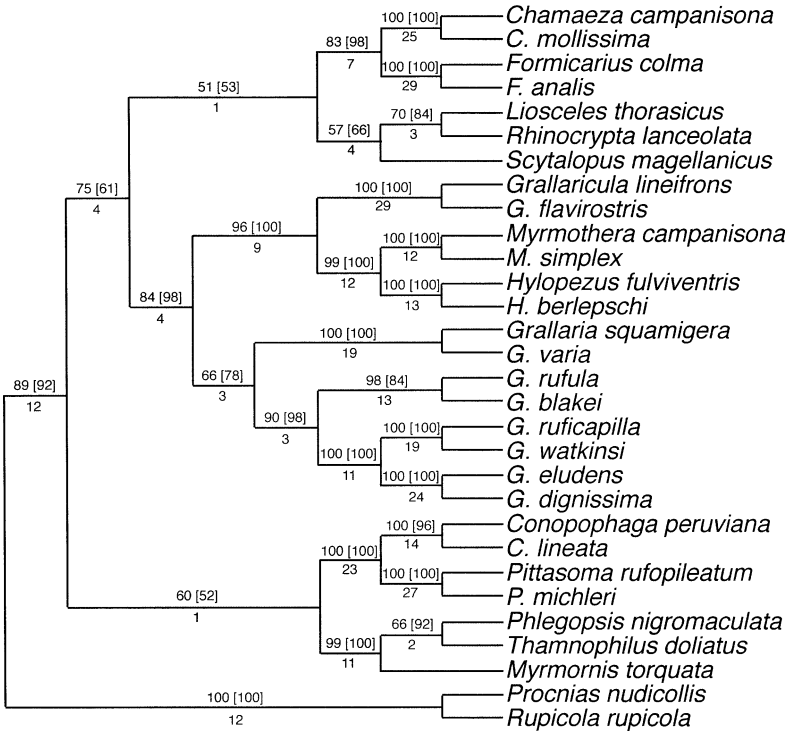

FIGURE 1. Most parsimonious (majority rule consensus) and most likely tree topology of the combined molecular dataset for the ground antbirds. Numbers above each internode refer to bootstrap values (maximum likelihood bootstrap values in brackets). Numbers below each internode refer to Bremer Decay Indices.

Myrmothera is the sister genus to *Hylopezus*, and *Grallaricula* is their sister genus. The second antpitta clade is the large and complex genus *Grallaria*. Within *Grallaria*, *G. eludens* + *G. dignissima* is the sister lineage to *G. ruficapilla* + *G. watkinsi*, and *G. rufula* + *G. blakei* forms their sister lineage. The large bodied antpittas, *G. squamigera* + *G. varia*, formed the basal lineage of the *Grallaria* clade.

Within the larger ground antbird lineage, the antthrushes and tapaculos were weakly supported as sister taxa. In this clade, the antthrush genera *Formicarius* and *Chamaeza* were found to be monophyletic and each other's sister taxa. The three tapaculos sequenced for this study formed a monophyletic lineage with *Liosceles*, the sister to *Rhinocrypta*, and *Scytalopus* as their sister taxa.

DISCUSSION

One of the best-resolved and well-supported clades in this study was the antpitta lineage. It is interesting to note that the ''antpitta'' genus *Pittasoma* is strongly supported as the sister genus to *Conopophaga*, a relationship that is reinforced by several important morphological and vocal synapomorphies (Rice 2005). Following the results of Irestedt et al. (2002) and Chesser (2004), this study does not support a close relationship between antpittas and antthrushes, contra Sibley and Ahlquist (1990). In fact, average pairwise sequence divergence between antpittas and antthrushes was 22.5%, on the same order as that between typical antbirds and antthrushes (22.7%). In this study, the antthrushes were monophyletic and sister to the tapaculos.

The antpittas constitute one of the two major ground antbird clades. This group is identical to the Grallarinae of Lowery and O'Neill (1969), with the exclusion of *Pittasoma*. Within the antpitta clade are two well-supported sublineages: (1) the large and complex genus *Grallaria*, and (2) the generally smaller antpittas *Grallaricula*, *Myrmothera*, and *Hylopezus*. Members of both subclades hop on the ground in an upright position, have short tails, deep and robust bills, holospidean tarsal scutellation, and generally lay round bluish or greenish eggs (Lowery and O'Neill 1969, Fjeldså and Krabbe 1990, Sick 1993). The evolutionary history and morphological character evolution within the antpitta clade has been discussed elsewhere (Rice 2000, 2005).

Not surprisingly, the antthrush genera *Formicarius* and *Chamaeza* were placed as sister taxa. According to Ames et al. (1968), the antthrushes have unique spinal pterylae, heavily feathered in the posterior region, compared with other tracheophones. Natural history information is lacking for many antthrush taxa, although for the species that have been examined, all have spherically shaped white eggs. In addition, *Formicarius* and *Chamaeza* antthrushes also both nest in tree cavities (Fig. 2, Krabbe and Schulenberg 2003).

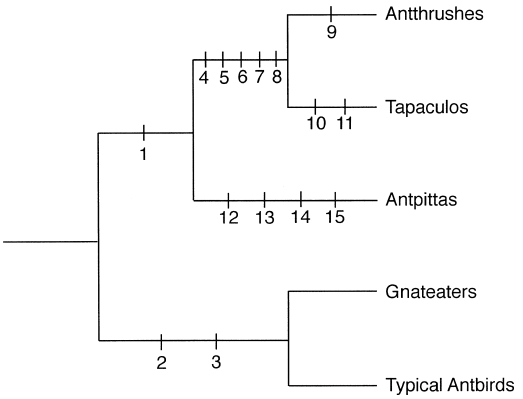

FIGURE 2. Simplified tree derived from the molecular phylogeny in Figure 1. Major lineages have been pruned to a single branch and common name moniker. Major morphological features discussed in the text and coinciding with the molecular phylogeny are mapped onto the tree. Numbers refer to the following characters: (1) simple insertion of the musculus sternotrachealis; (2) sexual dichromatism; (3) exaspidean tarsal scutellation; (4) whitish colored eggs; (5) walking is primary locomotion; (6) long tail held cocked; (7) taxaspidean tarsal scutellation; (8) nest placed in cavity; (9) heavily feathered dorsal pterylae; (10) dorsal origination of musculus vocalis; (11) unseparated lateral pterylae; (12) bluish/greenish colored eggs; (13) short tail held straight; (14) hopping is primary locomotion; (15) holospidean tarsal scutellation. Note that the clade labelled ''tapaculo'' does not include *Melanopareia* (following Irestedt et al. 2002) and the ''gnateater'' clade includes *Pittasoma* (following Rice 2005).

Given the morphological diversity within the Rhinocryptidae and among those included herein, it was interesting to find that the three genera included in this study formed a monophyletic lineage. All known tapaculo nests are enclosed structures, placed in burrows, holes, or crevices (Fjeldså and Krabbe 1990, Ridgely and Tudor 1994). Rhinocryptid syringes (at least those described) are similar to those found in ground antbirds, but have the derived feature of a dorsally originating musculus vocalis (Ames 1971). In addition, tapaculo pterylae are unique among tracheophones, in that they are unseparated in the flank margin (Fig. 2, Ames et al. 1968).

Although only weak molecular support exists for placing *Liosceles* + *Rhinocrypta* + *Scytalopus* as sister to the antthrushes, several interesting morphological synapomorphies support this relationship (Fig. 2). Members of both groups walk on the ground in a horizontal posture and have relatively long tails that are often held cocked, an apparently derived condition in the tracheophones (antpittas have very short tails and typical antbirds generally have tails of intermediate length that are held parallel to the main axis of the body). Tapaculos and antthrushes lay white eggs, in contrast to the bluish or greenish antpitta eggs. Most antthrushes and tapaculos also place their nests in some sort of cavity, either actively excavated or natural (e.g., rotten stump, tree root masses). Species of antthrushes and tapaculos also have taxaspidean tarsal scutellation, in contrast to the antpittas, which are holospidean. Although only three of 12 rhinocryptid genera were represented in this study, much of the diversity of the group was included, except for the aberrant *Psiloramphus* and *Melanopareia*. Inclusion of some or all rhinocryptids upon detailed study within the larger ground antbird clade may in the end prove reasonable, making Formicariidae paraphyletic.

Analyzing more molecular characters, but including fewer taxa, Irestedt et al. (2002) also found weak support for a sister relationship between tapaculos (excluding *Melanopareia*) and antthrushes. Chesser (2004) found that the ground antbird lineage was paraphyletic, but did not support a sister relationship between the tapaculos and antthrushes. Given that much of the phenotypic diversity of the Rhinocryptidae has been sequenced and found to be closely associated with antthrushes, it seems entirely feasible that the two groups are indeed sister taxa (regardless of the relatively weak statistical support in this study and in Irestedt et al. [2002]). In this case, the antthrushes and tapaculos would form a monophyletic family of suboscine passerines (Formicariidae) that is the sister lineage to a monophyletic antpitta family (Grallaridae, including *Grallaria*, *Grallaricula*, *Hylopezus*, and *Myrmothera*). It is also now well established that the family Conopophagidae should be redefined to include the former antpitta genus *Pittasoma*.

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AGE-BASED PLUMAGE CHANGES IN THE LANCE-TAILED MANAKIN: A TWO-YEAR DELAY IN PLUMAGE MATURATION

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Abstract. I investigated the relationship of plumage to age and sex in the Lance-tailed Manakin (Pipridae, *Chiroxiphia lanceolata*) in the lowlands of western Panama from 1999–2004. I captured birds in mist nets, categorized their plumages, examined them for molt, and followed them for several years to document plumage changes. Male Lance-tailed Manakins exhibited three distinct postjuvenal plumages. Males achieved definitive adult plumage through sequential changes that occurred in the same order as in other *Chiroxiphia* manakins. Definitive male plumage developed over the same time span as reported for *C. caudata* but one year faster than *C. linearis*. Juvenal male plumage was similar to that of females, and 5% of 226 females had plumage similar to formative male plumage. Genetic sexing verified that changes observed late in the formative male plumage unambiguously identified sex and age of individual birds. This information can be used in behavioral studies to identify the age of male Lance-tailed Manakins captured in any of the predefinitive plumage stages.

Key words: Chiroxiphia, *delayed plumage maturation, Lance-tailed Manakin, Panama, plumage development.*

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Cambios de Plumaje Relacionados con la Edad en *Chiroxiphia lanceolata*: Dos Años de Demora en la Maduración del Plumaje

Resumen. Investigué la relación entre el plumaje, la edad y el sexo en *Chiroxiphia lanceolata* (Pipridae) en el oeste de Panamá entre 1999 y 2004. Capturé aves con redes, clasifiqué sus plumajes, examiné la muda del plumaje y los observé durante algunos años para documentar cambios en su plumaje. Los machos presentaron tres plumajes post-juveniles distintos. Los machos alcanzan el plumaje definitivo adulto mediante cambios secuenciales que ocurren en el mismo orden en otros saltarines del género *Chiroxiphia*. El plumaje definitivo se desarrolló en el mismo tiempo que en *C. caudata*, pero un año más rápido que en *C. linearis*. El plumaje de los machos juveniles fue similar al de las hembras, y el 5% de 226 hembras presentó un plumaje parecido al plumaje formativo de los machos. Por medio de análisis genéticos de identificación de sexos, verifiqué que los cambios tardíos observados en el plumaje formativo de los machos permitieron identificar el sexo y la edad de los individuos sin ambigüedades. Esta información puede ser usada en estudios de comportamiento para identificar la edad de los machos con cualquier plumaje predefinitivo.

The Lance-tailed Manakin (*Chiroxiphia lanceolata*) is a small (15.5–22 g), mostly frugivorous passerine in the family Pipridae. This species inhabits lowland forests of southwestern Costa Rica, western Panama, northeastern Columbia, and northern Venezuela and is notable for the elaborate cooperative lek displays of males (Wetmore 1972, Ridgely and Tudor 1994). Like the majority of manakin species, *C. lanceolata* are sexually dimorphic. Adult males have a definitive male plumage of black body feathers with grayish-black rump, blue upper back, and a bright red cap of long narrow feathers. Females are olive-green with paler ventral regions, and some adult females have red or orange crest feathers (Wetmore 1972). Both sexes have bright orange legs, and dark brown or reddish-brown irises, and central rectrices that extend 5–18 mm beyond the length of the other tail feathers.

Young males pass through multiple predefinitive plumages before attaining their definitive adult plumage, but the number of years required for plumage maturation and the reliability of predefinitive plumages in indicating age and sex of individuals is unknown. Research in other *Chiroxiphia* manakins has demonstrated that the time required for plumage maturation varies across species (Foster 1981, McDonald 1993a). Furthermore, the difficulty of distinguishing young males from females has complicated the interpretation of dance displays in which birds that appear to be young males behave like females, or vice versa (Snow 1963, Foster 1981). Here, I describe the complete sequence of plumage changes with age in the Lance-tailed Manakin based on repeated captures of banded individuals over six years. This study is the first to use genetic sexing and recaptures of known-age individuals banded in the nest to confirm the relationship of age and sex to plumage aspect in a *Chiroxiphia* manakin.

METHODS

This study was conducted in a 46-ha area of secondary growth, dry tropical forest on Isla Boca Brava in Chiriquí Province, Republic of Panama (8°12′N, 82°12′W). Postfledging Lance-tailed Manakins were captured using mist nets and individually marked with a numbered aluminum and three colored plastic leg bands. All captured individuals were weighed, measured (tarsus length, unflattened wing chord length, nare to tip of bill, length and width of relaxed crest, tail length, and extension of the longer of the two central rectrices past the main tail), and scored for breeding condition (brood patch or cloacal protuberance). Plumage was categorized based on the color and morphology of crest feathers; presence and extent of black feathers on head, body, wings, and tail; presence and extent of blue feathers on back; and location and extent of growing, sheathed feathers indicative of molt. Limited, asymmetric feather replacement was considered to be adventitious and not part of a molt cycle. Between 1999 and 2004, 457 postfledging individuals were captured on the study site during a total of 2155 mist-net hours (one 12-m net open for one hour). Captures occurred between March and July, a time period that includes the peak of breeding activity at this site (EHD, unpubl. data). An additional 132 individuals were banded as nestlings.

TERMINOLOGY

Molt and plumage terminology follow Humphrey and Parkes (1959) as modified by Howell et al. (2003), with genus-specific classifications analogous to those of McDonald (1993a). I use the term ''predefinitive'' rather than ''subadult'' to denote postjuvenal plumages that change with age, as I have no data on the reproductive competence of young males (Humphrey and Parkes 1959, Foster 1987). Age classes follow Pyle (1997), such that a second-year (SY) bird is in its second calendar year (1 January of the year following fledging through 31 December of the same year). Only physical captures of individuals were considered in constructing the plumage maturation order, as intermediate plumage stages can appear similar when viewed through binoculars under some light conditions. Molt generally began toward the end of the breeding season, so that a male in one subadult plumage during the breeding season of its second year would molt into the next plumage (which it maintained through the breeding season of its third year) while still a second-year bird. Because I observed plumage primarily in the breeding season, I describe plumage-linked age classes as they are observed during the breeding season.

GENETIC SEXING

Because some females have plumage characteristics similar to those of young males, females were identified by the presence of a brood patch or were sexed using molecular techniques. All individuals that had no brood patch when captured in sexually ambiguous plumages were genetically sexed. Individuals captured with black facial plumage or more extensive male plumage characters were assumed to be male, and this was confirmed by genetically sexing 47 individuals in different male plumage categories. DNA was extracted

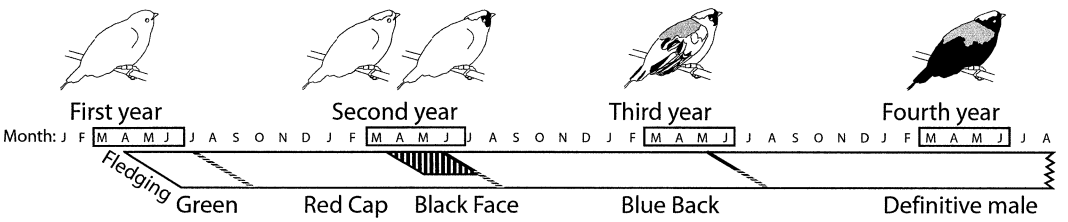

FIGURE 1. Timeline of plumage stages and molt in *Chiroxiphia lanceolata*. Molts are represented by diagonal lines between plumages, corresponding to the range of months in which these molts occurred. Dashed lines indicate estimated time range for molts that were not completely observed due to field season schedules. The cross-hatched portion of the timeline represents the Black Face plumage, which results from a partial molt of facial feathers. Boxed months indicate the beginning and peak of the breeding season, during which most field seasons in this study were conducted.

from whole blood preserved in Longmire's blood buffer solution (Longmire et al. 1988), and sex was determined from a PCR reaction that amplifies the CHD genes on the W and Z chromosomes using primers P2 and P8 (Griffiths et al. 1998). Reaction conditions were as described in Griffiths et al. (1998), using an annealing temperature of 56°C. PCR products were separated by electrophoresis on a 2% agarose gel and stained with ethidium bromide.

STATISTICAL ANALYSES

Measurements for individuals captured more than once in the same year were averaged, and each male was included only once in the measurement data set. For individuals with multiple years of data, I randomly selected one year of data to include. Measurements were not normally distributed and could not be transformed to normality, so I tested for differences among age classes using Kruskall-Wallis tests. When the test indicated significant deviation from the null hypothesis, I tested for significant differences between age categories using Dunn's nonparametric multiple comparisons test for unequal sample sizes (Zar 1999). Data are presented as mean ± one standard deviation.

RESULTS

MOLTING STRATEGY

Lance-tailed Manakins follow a complex basic molt strategy (Howell et al. 2003), with molt and breeding occurring as an annual cycle (Fig. 1). The main molting period begins approximately in June and continues past the end of my field seasons in July. Body feathers of young birds are replaced approximately 2–3 months after fledging in a preformative molt. Feather wear on young birds captured later in their first year suggests that this molt is partial, with remiges and rectrices retained, but the completion of this molt was not observed due to field season schedules. Subsequent ages have complete prebasic molts that begin in June to July of each year. Like other manakins, this species lacks alternate plumages.

MALE PLUMAGE STAGES

Lance-tailed Manakins have definitive adult plumage in the breeding season of their fourth year, after two prebasic molts (Fig. 1, Table 1). Forty-four males were captured at least once while in a predefinitive plumage and again in the consecutive year. Nine of these 44 males were captured in juvenal and both predefinitive plumages. All observed plumage changes by these males agreed with the sequence described below.

Juvenile male Lance-tailed Manakins are green overall, although males may have an orangeish cap of feathers morphologically indistinct from other head feathers (''Tawny Cap'' plumage). The formative male plumage (''Red Cap'') consists of green body feathers, remiges, and rectrices, and a cap of shiny red feathers that are longer and narrower than their other head feathers. This crest initially grows in a ''V'' of two feather tracts along the top of the head that diverge posteriorly, giving the crest a ''split'' appearance. Second-year males attain black lores by the end of the breeding season, with black sometimes extending onto the face (''Black Face'' plumage). The development of Black Face plumage is somewhat variable in timing, but develops after 10–12 months of age. Eleven juvenile males initially captured in Green, Tawny Cap, or slight Red Cap plumage and recaptured in the following year, molted into Red Cap or Black Face plumage in the intervening 8–10 months (mean = 8.7 ± 0.9 months).

The second prebasic molt begins at approximately 13–15 months posthatching. The resulting second basic male plumage (''Blue Back'') comprises a red cap, black face, green-and-black body feathers giving a mottled appearance, scattered blue or partially blue feathers on the back, and variably dark remiges and rectrices. Several of the secondaries or rectrices of these birds are usually black or half black. Twenty-seven males initially captured in Red Cap or Black Face plumage were recaptured in the following year and had molted into Blue Back plumage in the 7.5–13.5 months (mean = 11.3 ± 1.9 months) between captures.

At the third prebasic molt (approximately 26 months posthatching), males attain definitive plumage. Males in their first year of this definitive male adult plumage can have slightly more greenish-black body feathers than males in subsequent years, but these greenish definitive males are indistinguishable from darker males in the field. Sixteen males captured in Blue Back plumage were recaptured in the following year and had molted into definitive male plumage in the 10–14 months (mean = 12.3 ± 1.6 months) between captures.

TABLE 1. Categorization of Lance-tailed Manakin plumages from six years (1999–2004) of field studies in the Republic of Panama. In all, this represents 570 plumage-captures of 467 postfledging individuals.

Plumage[a]	Aspect	Description	Age class[b]	Sex[c]
Juvenal	Green	Olive-green body and flight feathers; may or may not have longer crest feathers, but these are also olive green	HY male/female or AHY female	1 male; 199 females; 13 unknown
	Tawny Cap	Orangeish crest feathers, may or may not be morphologically distinct from other head feathers	HY male or AHY female	8 males; 46 females
Formative	Red Cap	Red, elongated crest feathers; green body and head feathers	SY	56 males; 11 females
	Black Face	Red Cap plumage with some black feathers around lores		45 males; 0 females
Second basic	Blue Back	Red cap, some black on head, scattered blue on back	TY	72 males; 0 females
Third basic	Definitive male	Red cap, black head and body, blue on back	ATY	132 male; 0 females

[a] Plumage terminology follows Humphrey and Parkes (1959). Plumage-type names follow McDonald (1993a).
[b] HY = hatch year; AHY = after hatch year; SY = second year; TY = third year; ATY = after third year. Age classes follow Pyle (1997), such that a SY bird is in its second calendar year.
[c] Numbers indicate unique individuals captured in each plumage class by sex. Individuals captured in more than one plumage are counted in each observed plumage stage. Sex was determined as described in methods. All Tawny Cap males were genetically sexed, and five of these eight males were additionally sighted in a later male plumage. Thirteen green-plumaged birds of unknown sex were not genetically sexed.

CAPTURES OF KNOWN-AGE INDIVIDUALS

This general plumage sequence is further confirmed by captures of twelve male chicks banded in the nest that were later captured one or more times in mist nets, providing information on plumage stage for males of precisely known age (Table 2). One of these males was captured at two months of age with Tawny Cap plumage; one male captured at nine months of age had Red Cap plumage, with the cap incomplete in ''split'' formation; seven males captured at 10–12 months of age were in Black Face plumage; two males captured at 12–13 months of age showed small amounts of blue feathers on the back; four males captured at 24.5–25.5 months had typical Blue Back plumage; and one male captured at 35 months was in full definitive male plumage. The plumage stages of these known-age birds were consistent with the general order and progression of plumages in other young males.

VARIATION IN FEMALE PLUMAGE

Young female Lance-tailed Manakins retain uniformly green plumage after the preformative molt, and this is the definitive plumage of most females. The majority of females (78% of 226 individuals) had completely green plumage as described in Wetmore (1972). A small proportion of individual females had male-like plumage, as reported in some other manakin species (Foster 1981). Approximately 5% of all females had Red Cap plumage, and an additional 17% of females had Tawny Cap plumage. Tawny Cap birds frequently had only a few orangeish feathers in their crests, and were usually classed as green-plumage when sighted with binoculars. The majority of females did not change plumage type between years, but two females initially captured with slight Tawny Cap plumage gradually developed full red crests over two to three breeding seasons. The actual age of females was generally unknown, as most were captured as unbanded immigrants from outside of the field site. Three females banded as chicks were recaptured on the study site, and had completely green plumage at 12.5–13 months of age.

GENETIC SEX BY PLUMAGE TYPE

Genetic sexing of 47 individuals in Black Face or later male plumage confirmed that all were male (9 Black Face, 14 Blue Back, and 24 definitive male). The genetic sex of birds in Green, Red Cap, and Tawny Cap plumage was examined on a per-capture basis, as males were frequently recaptured in later plumage stages. Females represented 16.4% of 67 Red Cap captures, 85% of 54 Tawny Cap captures, and 99.5% of 213 birds in Green plumage (Table 1).

CHANGES IN PLUMAGE MORPHOLOGY WITH AGE

Several changes in plumage morphology were linked with age in young males. I examined differences in plumage characteristics of known-age birds aged by capture in predefinitive plumage and found that the length of r1 (the longest extended middle rectrix) was significantly different among age classes ($df = 3$, $Z = 63.3$, $P \leq 0.001$), as were the area of the red crest ($df = 2$, $Z = 26.8$, $P \leq 0.001$) and wing chord length ($df = 3$, $Z = 66.0$, $P \leq 0.001$; Fig. 2). Multiple comparisons indicated that third- and fourth-year males were significantly different from younger birds in wing

TABLE 2. Plumage stage of 12 males banded in the nest and later recaptured.

Individual	Hatch date	Recapture date	Age (months)	Plumage at recapture[a]
248	18 Apr 2000	26 Mar 2001	11	BF (slight)
		28 Apr 2001	12	BF (slight)
249	18 Apr 2000	31 May 2002	25.5	BB
		06 Jun 2002	25.5	BB
283	05 May 2000	10 Apr 2001	11	BF (slight)
		23 Apr 2001	11.5	BF
		26 Apr 2002	23.5	BB
		19 May 2002	24	BB
287	10 May 2000	26 Mar 2001	10	BF (slight)
		07 May 2001	12	BB (slight)
		17 Jun 2001	13	BB (slight)
302	23 May 2000	22 Jun 2001	13	BB
		30 May 2002	24	BB
374	20 Apr 2001	21 Jun 2001	2	TC
		25 Jun 2001	2	TC
403	06 May 2001	03 Apr 2004	35	DM
422	26 Apr 2001	27 Apr 2002	12	BF (slight)
444	13 Jun 2001	26 Mar 2002	9	RC (split)
466	10 Apr 2002	09 Apr 2003	12	BF (slight)
		29 Apr 2003	12.5	BF (slight)
		03 Apr 2004	24	BB
535	16 Jun 2002	08 Apr 2003	10	BF
546	17 Jun 2002	10 Apr 2003	10	BF (slight)

[a] Plumage-stage codes are as follows: BF = Black Face, BB = Blue Back, TC = Tawny Cap, DM = Definitive male, and RC = Red Cap. ''Slight'' indicates plumage which meets the plumage stage definitions in Table 1 but which may be mistaken for the previous plumage when viewed with binoculars. ''Split'' indicates a V-shaped, developing red cap with feathers emerged in two distinct tracts on the head.

chord and cap area ($P \leq 0.05$ indicated by $Q_{0.05,5} > 2.8$), but not different from each other. Third- and fourth-year males were different from each other and from younger birds in tail extension length (Fig. 2).

DISCUSSION

Predefinitive male plumages in the Lance-tailed Manakin are reliable indicators of age for second-year (Red Cap or Black Face) and third-year (Blue Back) males. Furthermore, individuals in Black Face and later plumages are unambiguously male. The majority of females have all-green plumage, although some have orangeish or red caps indistinguishable from those of hatch-year or second-year males.

Throughout the genus *Chiroxiphia*, the acquisition of adult male plumage elements occurs in the same general order: males start with a green base plumage; then gain a cap of elongated red feathers; next black feathers on the face or lores; then blue back feathers and some black body, tail and flight feathers; and finally replace remaining green with black or blue feathers (Foster 1987, McDonald 1993a). The timing of molts and overall length of time to attain adult male plumage in *C. lanceolata* is more similar to *C. caudata* (Foster 1987) than to *C. linearis* (McDonald 1989). Male *C. caudata* (Foster 1987) and *C. lanceolata* attain definitive plumage by the breeding season of their fourth year, while *C. linearis* attain definitive adult plumage by their fifth year (Foster 1977, Foster 1987, McDonald 1993a). The timing of the Red Cap, Black Face, and Blue Back plumage stages in *C. linearis* is debated. Foster (1987) reported that the Red Cap and Black Face stages occur in only one year class (second-year), and she separated Blue Back males into two year stages (third- and fourth-year). McDonald (1993a) divided Red Cap and Black Face males into two age classes (second- and third-year), but combined all Blue Back males in one age class (fourth-year). This study demonstrates that in *C. lanceolata*, the Red Cap and Black Face plumages are included within one age class and molt stage, as reported for *C. caudata*. Also as in *C. caudata*, Blue Back males in *C. lanceolata* are defined by one molt and age class, though the extent of blue on the back and the degree of dark body feathers and remiges varies by individual and may change during a protracted molt.

Species-level differences in delayed plumage maturation may be related to differences in the time required to attain a breeding position (Foster 1987, McDonald 1993b). Only males of alpha or beta status perform courtship displays for females (McDonald 1989), and alpha and beta males in *C. linearis* are usually at least 8 years old (McDonald 1993b). In contrast, male *C. lanceolata* may become betas at 4 or 5 years of age (EHD, unpubl. data).

My results demonstrate that the plumage of young male Lance-tailed Manakins may be used to estimate reliably the age of individuals captured in any of the distinct predefinitive plumage classes. This is of particular utility in long-term studies of banded individuals, as plumage can be used to determine accurately the age of adult males previously captured in predefinitive plumages.

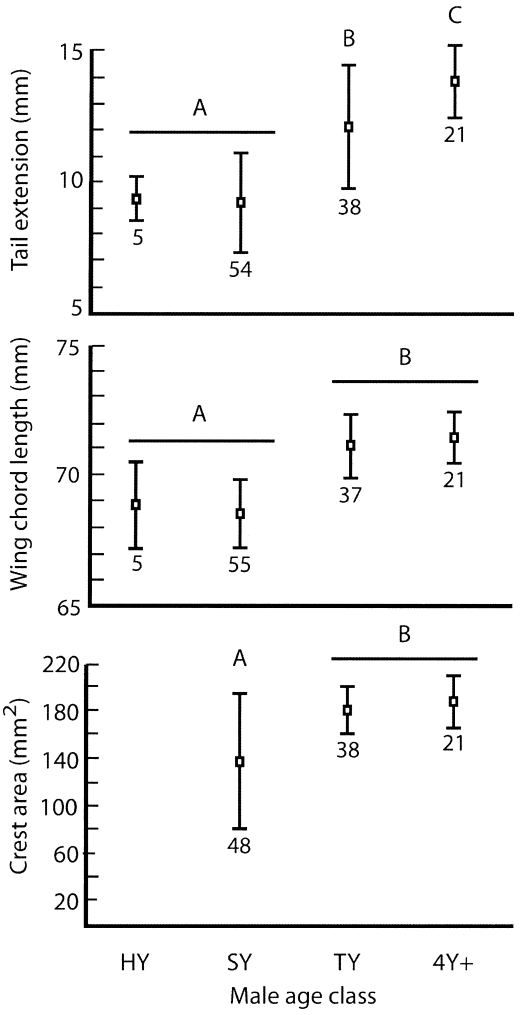

FIGURE 2. Differences in male plumage morphology by age class. Hatch-year and second year males have shorter central rectrices and wing chord lengths than males in their third year or older. Second-year males also have significantly smaller crest areas than older males. Letter codes indicate that groups differed significantly ($P \leq 0.05$, Dunn's nonparametric multiple comparisons test for unequal sample sizes, Zar 1999). Codes for age classes refer to Table 1. Graphs represent mean (± SD) of plumage measurements with sample sizes shown below each bar. Males of known age in their fourth ($n = 15$) and fifth ($n = 6$) years were pooled into one age class, 4Y+.

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