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THE CURRENT STATE OF KNOWLEDGE ON MOLT AND PLUMAGE SEQUENCES IN SELECTED NEOTROPICAL BIRD FAMILIES: A REVIEW

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Resumen. – El estado de conocimiento actual en mudas y secuencia de plumajes en ciertas familias tropicales: una revisión. – Las mudas anuales y sus subsecuentes plumajes se encuentran ampliamente representados en la historia de vida de las aves. La investigación relacionada a la utilidad de mudas y plumaje ha producido un marco conceptual confiable para la caracterización de edad en la mayoría de la avifauna de la zona templada. En comparación a la zona templada; sin embargo, conocemos muy poco sobre las mudas y plumajes de las aves tropicales residentes. Los datos publicados con respecto a mudas y secuencias de plumaje son limitados en rango, cubren pocas especies, y, hasta nuestro entendimiento, no están actualmente resumidos. Aquí combinamos nueva información recolectada en trabajo de campo y en museos con una síntesis de un trabajo previo para revisar muda y plumaje para 15 familias de paserinos y cuasi-paserinos del Nuevo Mundo. Específicamente, resumimos secuencias y extensión de mudas debido a que se encuentran relacionadas con la categorización de edad; además, asignamos estrategias de muda generales basadas en patrones encontrados entre géneros dentro de cada familia. Dada la diversidad de la mayoría de familias de paserinos tropicales, este resumen no incluye a todas ellas; sin embargo, lo presentamos como un marco conceptual amplio con el fin de incrementar nuestro entendimiento de la muda y secuencia de plumaje en la avifauna tropical.

Abstract. – Annual molts and the subsequent plumages they produce are a ubiquitous element of avian life history. Research pertaining to the utility of molt and plumage has produced a robust framework of age-categorization for the vast majority of temperate avifauna. In comparison to temperate bird species, however, we know very little about resident tropical bird molt and plumage. Published data pertaining to molt and plumage sequences are limited in scope, covering few species, and, to our knowledge, are not currently synthesized. Here we combine new information gathered from field and museum specimens

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with a synthesis of previous work to review molt and plumage for 15 families of New-World tropical passerines and near-passerines. More specifically, we outline plumage sequences and molt extent as it relates to age-categorization; we also assign generalized molt strategies based on common patterns found among genera within each family. Given the diversity of most tropical passerine families, this synthesis is not all-inclusive; however, it is presented in a broad framework with the goal of advancing our knowledge of tropical avian molt and plumage sequences. *Accepted 19 November 2008.*

Key words: Molt, plumage, plumage-sequence, tropical, New World.

INTRODUCTION

The utilitarian value of molt and plumage sequences, as it pertains to aging birds, is well established in both Europe (Jenni & Winkler 1994) and North America (Mulvihill 1993). However, the applicability of these practices is wholly reliant on available information for families, genera and species of interest. In temperate North America, molt and plumage information on passerines and near-passerines have been summarized by Pyle (1997), which facilitates the placement of captured individuals into accurate and repeatable age classes. Despite recent advances in our understanding of molt and plumage development for temperate species, relatively little is known about resident terrestrial bird taxa in the Neotropics (Pyle *et al.* 2004). Moreover, there is a need for a new progressive system of age classification for tropical resident birds given the potential difficulties of applying the calendar-based age-classification system to tropical taxa (Wolfe *et al.* unpubl data).

The majority of work on molt in tropical resident birds has focused on the timing of molt in relation to other activities in the annual cycle (Snow & Snow 1964, Foster 1975, Poulin *et al.* 1992, Piratelli *et al.* 2000, Marini & Duraes 2001, Mallet-Rodrigues 2005) rather than duration and extent of molts, and progression of plumages (Pyle *et al.* 2004, Ryder & Durães 2005, Doucet *et al.* 2007). In families for which these data are available, information is limited to few species with the assumption that related species show similar characteristics. This assumption may

be warranted in species where a phylogenetic analysis of molt shows well-conserved patterns across closely related species (Hall & Tullberg 2004). Some related species that occur in different habitat types appear to have different molt strategies, which may be correlated with different environmental attributes (e.g., amount of solar radiation in open *vs.* shady habitats).

Previous studies suggest that most tropical residents have a single annual prebasic and partial preformative molt (Dickey & Van Rossem 1938, Piratelli *et al.* 2000, DuVal 2005, Mallet-Rodrigues 2005, Ryder & Durães 2005, Doucet *et al.* 2007). The existence of a partial preformative molt in many tropical taxa makes molt-based aging criteria (i.e., retained juvenile plumage, delayed plumage maturation and molt-limits) possible for tropical residents. Here, we present data compiled from contemporary literature, personal field observations, and review of museum specimens to summarize what is known about tropical bird molt. We use our findings to develop conservative estimates of molt strategy, extent, and associated plumage sequences (when available) for 15 Neotropical avian families. We also include information on other relevant characters that vary by age (i.e., eye and bill color).

METHODS

Field observations were made at two study sites in Central America and northern South America. The Central American site is located in Tourtuguero, Costa Rica (10°33'51"N,

83°31'7"W), in lowland Caribbean rain forest. Klamath Bird Observatory and Redwood Sciences Laboratory (USFS) have operated a monitoring station at five sites around Tortuguero since 1994 (Ralph *et al.* 2005). Both authors served as primary banders at these stations for a total of three years, during which time information on molt and plumage sequence was compiled. The South American site is located in eastern Ecuador at the Tiputini Biodiversity Station (0°38'S, 76°08'W), also in lowland rain forest. TBR conducted his dissertation research at this site over the past five years, during two of which JDW was present; both authors documented plumage and molt information.

In addition to field observations, we visited museum bird collections to document plumage sequences and the extent of molt in previously unstudied tropical families. We visited the Field Museum of Natural History in Chicago ($n = 3522$ specimens), California Academy of Sciences, Department of Ornithology and Mammalogy, San Francisco ($n = 477$) and the Smithsonian National Museum of Natural History, Washington, D.C. ($n = 589$).

Here we chose to examine 14 families, 1 subfamily, and 106 genera based on their diverse taxonomic relationships and the availability of previously published molt and plumage data. Given the astounding diversity of tropical taxa not all representative families could be included. All taxonomic assignment included in this paper follow the recommendations of the AOU South American Classification Committee. The subfamily Dendrocolaptinae was included because of its diversity and distinct molt and plumage patterns.

To limit confusion, promote molt homologies across taxa, and encourage non-ambiguous nomenclature, we have used modified Humphrey-Parkes terminology (Howell *et al.* 2003). The most relevant terminological changes are the renaming of the traditional

'prejuvenile molt' as the 'first prebasic molt,' and the traditional 'first prebasic molt' as the 'preformative molt.' Molt and their corresponding cycles are named for the plumage they produce (e.g., the preformative molt produces the formative plumage). We use the term 'juvenile' in place of 'first basic' because the former is more widely recognized. Also of note is the use of 'definitive' instead of the more commonly used 'adult' to describe plumage and molt cycles associated with later phases of a bird's life cycle. The term 'definitive plumage' describes attainment of plumage maturation (e.g., a *Pipra filicauda* male after the third prebasic molt has attained definitive plumage). The term 'adult' often implies sexual maturity, which typically has no relevance when considering plumage maturation or molt (e.g., a formative plumaged *Setophaga ruticilla* male is in a predifinitive plumage, yet, it is capable of breeding and can be considered sexually an 'adult' or 'mature'). Following Howell *et al.* (2003), we have assigned families to molt strategies: either Complex Basic Strategy (CBS), Complex Alternate Strategy (CAS), or both.

RESULTS

Molt and plumages of tropical families

Trogonidae (CBS and CAS). The juvenile plumage in Trogonidae is variable, with some species in the genus *Trogon* having spotted plumage (Dickey & van Rossem 1938), buffy-tipped flight-feather coverts, brownish overall plumage, barred and/or spotted underparts (Stiles & Skutch 1989).

Apparently all *Trogon* species retain all or some of their rectrices during the preformative molt. Formative plumage in Trogonidae generally resembles either female definitive plumage, or respective definitive plumage (Dickey & van Rossem 1938). Evidence from museum skins suggests that all formative

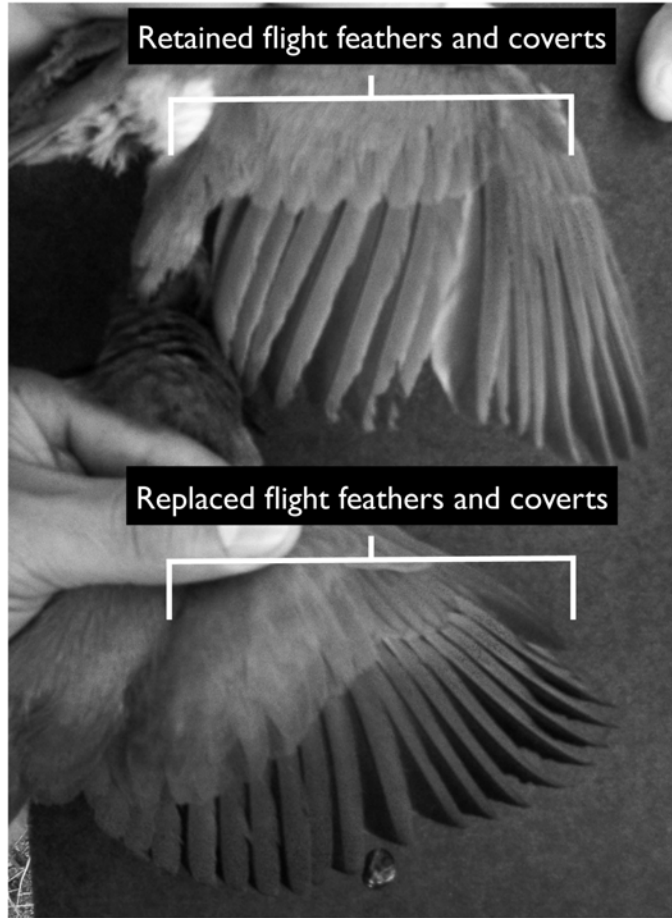


FIG. 1. Formative plumage (top) and definitive plumaged (bottom) *Motmotus mexicanus* can be distinguished by the wear and coloration pattern of retained flight feathers and coverts (photo: P. Pyle).

plumaged Trogonidae typically have distinctly retained tails, and/or a differential amount of iridescence in body and head plumage in relation to definitive plumage. Some species within the genus *Trogon* (e.g., *T. elegans*) have age-specific tail patterns (see Pyle 1997). The preformative molt in *Euptilotis neoxenus* and some *Trogon* species can be incomplete, including the tertials and one or more secondaries. Interestingly, in *E. neoxenus*, definitive prebasic molts can retain one or more sec-

ondaries and one or more rectrices (Pyle 1997). Definitive prebasic molts in most species appear to be complete. Rectrix replacement in *Trogon sallaei* and *T. elegans* may be unique where some individuals molt the central tail feathers first, and others the lateral ones. In some instances these species may replace one entire side before the other (Dickey & van Rossem 1938). The prealternate molt can be limited to the head, upperparts or back in *T. melanocephala*, *T. sallaei*, and

T. elegans. Additionally, Pyle (1997) found that northern populations of *T. elegans* lack a prealternate molt. Prealternate molts in other trogonids are undocumented.

Momotidae (CBS). Evidence from museum skins suggests that juvenile plumage in *Electron*, *Eumomota*, *Baryphthengus*, *Hylomanes*, and *Momotus* are typically duller, sometimes lacking tail-rackets (when appropriate) and central breast spots (Dickey & van Rossem 1938, Stiles & Skutch 1989, Howell & Webb 1995).

Rectrices and possibly flight feathers appear to be universally retained during the preformative molt across the family. Dickey & Van Rossem (1938) describe *Momotus* and *Eumomota* as having a preformative molt, which lasts no more than two months. Flight feathers and rectrices are retained until the second (definitive) prebasic molt (Fig. 1). Retained first prebasic rectrices are easily distinguishable by their brown slate color and terminally tapered shape, where definitive central rectrices are more truncate. Retained juvenile flight feathers are washed brownish. Other than retained flight feathers and rectrices, definitive plumaged and formative plumaged birds appear similar. Protracted definitive prebasic molts in *Momotus* and *Eumomota* conclude with the flight feathers, and finish at the same time as the rectrices (Dickey & van Rossem 1938). There appears to be no prealternate molt in this family.

Bucconidae (CBS or CAS). Juvenile plumages are reportedly often indistinguishable from definitive plumages, although juvenile plumages in *Bucco*, *Malacoptila*, and *Hyphenelus* museum skins are typically duller with prominent plumage markings greatly reduced. In comparison, juvenile individuals of *Monasa* are more readily distinguishable, with a body plumage being heavily veiled grayish-brown as compared to the glossy black definitive plumage. In addition, *Monasa* species show age

variation in bill coloration. Subadult individuals are marked by an incomplete color pattern, with dull orange to yellow mandibles, which are distinguishable from the adults more uniform bill coloration.

Evidence for several genera suggests that the preformative molt in *Bucconidae* is either complete (e.g., *Notharcus*, *Bucco*, and *Malacoptila*) or sometimes uniquely incomplete (e.g., *Notharcus hyperrhynchus*; Dickey & van Rossem 1938). The preformative molt in *Notharcus hyperrhynchus* is characterized by scattered replacement of secondaries and/or primaries. In addition, this species has unique feather replacement patterns during definitive prebasic molts as well as an incomplete prealternate molt which includes all body plumage, irregular replacement of tertials, inner primaries, and rectrices (Dickey & van Rossem 1938). Investigation of museum skins for three species of *Monasa* (e.g., *M. atra*, *nigrifrons*, and *morpheus*) revealed retained greater, median, and lesser coverts in a mixed pattern. The retained coverts show extensive wear and discoloration and are easily differentiated from fresh coverts. Despite the apparent retention of primary and secondary coverts, no retained flight feathers or rectrices have been documented. Lesser, median, and greater coverts are either retained during an incomplete preformative molt or during an incomplete prealternate molt. The lack of retained flight feathers and rectrices point to a partial or incomplete prealternate molt, which could create a mixed-wear pattern in the coverts. Specimen evidence for other bucconids, however, suggests a single annual molt. The unique feather replacement patterns as described by Dickey & van Rossem (1938) may account for mixed age and wear in the greater coverts of bucconids.

Thamnophilidae (CBS). Juvenile plumage resembles female plumage (Zimmer & Isler 2003), although subtle differences in coloration

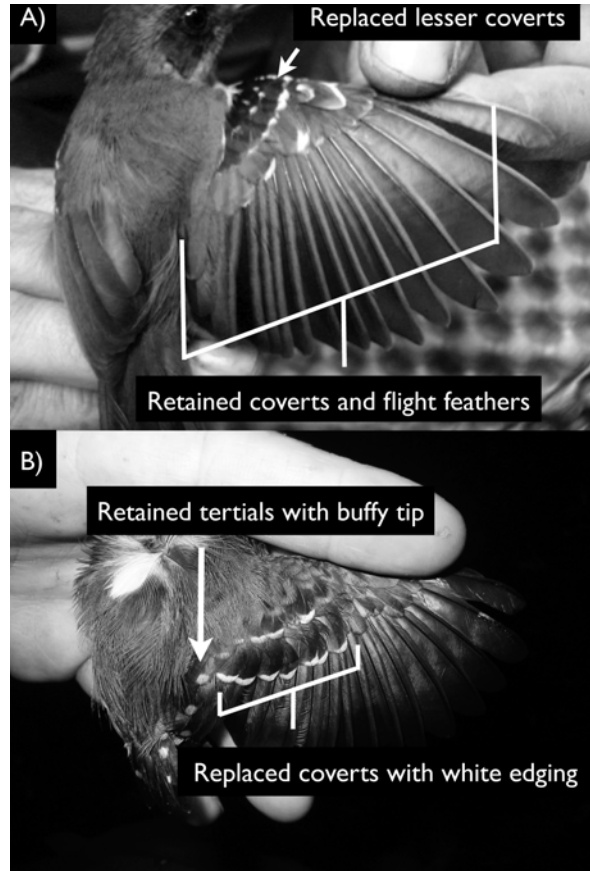


FIG. 2. A) Formative-plumaged male *Dysithamnus mentalis* showing replaced lesser coverts and retained flight feathers and greater, primary, median coverts; B) formative plumaged *Myrmotherula huxwelli* showing replaced greater coverts with a broad white edging. Note that retained juvenile tertials and outer greater coverts in many *Myrmotherula* species have a buffy orange coloration.

tion, as in Pipridae, may be detected with further study. See Howell & Webb (1995) for genera specific details on *Taraba*, *Thamnophilus*, *Dysithamnus*, *Microphias*, and *Cercromacra*. The duration of these juvenile plumages remain undocumented but are likely to last no more than one to two months.

Subsequent preformative molts are partial for many genera (e.g., *Taraba*, *Thamnophilus*, *Neotantes*, *Dysithamnus*, *Thamnomanes*, *Myrmotherula*, *Dichrozona*, *Herpsilochmus*, *Formicivora*,

Drymophila, *Terenura*, *Cercromacra*, *Myrmoborus*, *Hypocnemis*, *Peronostola*, *Schistocicla*, and *Hylaphylax*) and males may not attain definitive plumage until their second or possibly third prebasic molt. Some genera have eccentric or incomplete preformative molts (e.g., *Cymbilium*, *Pygptila*, *Microphias*, and some species of *Myrmoborus*, *Formicivora*, and *Cercromacra*) while other genera appear to have complete preformative molts (e.g., *Gymnopathys*, *Rhegmatorbina*, *Scelateria*, *Pyriglena*, and *Phlegopsis*). Formative

plumages in thamnophilids are more easily recognized in males, which show a mixture of male and juvenile (female type) plumage (e.g., *Hylophylax*, *Myrmeciza*, *Myrmoborus*, *Myrmotherula*, *Thamnophilus*, *Thamnomanes*, etc.) indicating delayed plumage maturation (Zimmer & Isler 2003). However, the extent of male plumage gained during the preformative molt varies individually and by genera. The extent of the partial preformative molt in this family is variable, but is most broadly characterized by replacement of body feathers, lesser and median coverts, and a variable number of inner greater coverts while outer greater coverts, primary coverts, alula, rectrices, and flight feathers are retained (Fig. 2A). In some genera, alula's may be replaced (e.g., *Hylophylax*), but this pattern needs further documentation. Taxa with incomplete (or possibly eccentric) preformative molts typically replace one to three tertials, a variable number of outer secondaries, and a variable number of inner primaries. In all cases, the corresponding primary coverts are also replaced. The retention of juvenile feathers in formative-plumaged thamnophilids is distinct, thereby facilitating easy recognition of molt limits. Replaced coverts have distinct broad edging in many taxa, which contrast markedly with retained juvenile coverts that differ in color and extent of edging. For example, in *Myrmotherula* species with wing bars and tertial tipping (e.g., *M. huxwelli*, and *axillaris*, etc.) retained juvenile tertials and coverts have a buffy orange coloration compared with white tips and edging of adult feathers (Fig. 2B). No prealternate molt has been documented in this family.

The timing of molt and breeding appear to overlap greatly in this family (Snow & Snow 1964, Foster 1975). However, overlap data may be inconclusive because individuals captured in breeding condition while undergoing a corresponding molt were not used to estimate overlap frequency. The data may

indeed suggest an overlap of annual activities or high asynchrony in annual activities (see Mallet-Rodrigues & de Noronha 2001).

Rhinocryptidae (probably CBS). Little is known about the plumage and molt patterns in tapaculos, which is in part due to the complexity of species identification of juveniles. The juvenile plumage in this family remains largely unknown. Barred juvenile plumages have been observed in the field (e.g., *Scytalopus*) and are also known from museum skins (e.g., *Myornis*, and *Engralla*). Juvenile plumages in *Rhinocrypta* specimens are similar to definitive plumages, except that the breast, throat, and crown stripes are washed buff, and small patches of buff are scattered on the back and uppertail coverts. Juveniles of *Scelorchilus* are similar to those of *Rhinocrypta*, except more heavily scalloped in buff on the flanks and uppertail coverts and scalloped white on the crown. Juveniles of *Myornis* are washed brownish with light barring on the tertials and uppertail coverts, while the juvenile plumage in *Pteroptochos tarnii* is generally darker rufous on the underparts. Additionally, specimens of the latter have white lower mandibles, which become completely black prior to the initiation of the preformative molt.

Several genera in this family exhibit complex and irregular plumage and molt patterns. Evidence from museum skins suggests that *Scytalopus*, *Myornis*, and *Engralla* may have successive molts after the preformative molt, resulting in one or two predelimitive plumages, but occasionally an individual may change directly into a nearly definitive plumage (Krabbe & Schulenberg 2003b). Possibly, individuals may undergo a two- to three-year transition into a predictable definitive plumage (e.g., *Scytalopus*, *Myornis*, and *Engralla*), facilitating accurate age categorization. Review of museum skins suggest that in other genera (e.g., *Melanopareia*, *Rhinocrypta*, and possibly *Scelorchilus*, and *Pteroptochos*) a transition to a

nearly definitive plumage occurs immediately after the preformative molt. The preformative molt in *Melanopareia*, *Rhinocrypta*, *Scelorchi-lus*, and *Pteroptocho* appears not to include flight feathers, primary coverts, and rectrices. No prealternate molt has been documented in the family.

Formicariidae (probably CBS). Juvenile plumages have been documented in a number of different genera (e.g., *Formicarius*, *Chamaeza*, *Grallaria*, *Myrmothera*, *Conopophaga*, *Pittasoma*, and *Grallariculla*) and have been described as being loosely textured (Krabbe & Schulenberg 2003a). Juvenile *Formicarius* in Mexico and Peru have sooty brownish throats and olive washed chests (Howell & Webb 1995, D. Lebbin pers. com.). Field observations of the genus *Grallaria* indicate a fluffy juvenile plumage that is replaced by a barred formative plumage (N. Krabbe pers. com., Krabbe & Schulenberg 2003a). However, the barred plumage may actually represent the juvenile stage, some of which is retained after the preformative molt. Juveniles may rather have very dark breasts, throat, crown, and nape, with white to buffy shaft streaks throughout the plumage as documented in *Grallaria guatimalensis* museum specimens. In *Conopophaga* species, juvenile plumages are characterized by barred or scalloped underparts, and at least one species (e.g., *C. lineata*) shows distinct rufous edging on the median and greater coverts. Juvenile-plumaged *Myrmothera* and *Grallaricula* have extensive buffy-tipped wing coverts, otherwise, juvenile plumage resembles definitive plumage. Lastly, juvenile *Pittasoma michleri* specimens exhibit a distinct ochraceous wash across the throat, with limited amounts of black in the throat, underparts washed buff, and limited to no white spotting on the wing coverts.

The extent of the preformative molt in *Formicariidae* is reportedly either partial or in some genera limited. Formative plumages

have been observed in Central American *Grallaria* (see Howell & Webb 1995). The preformative molt in *Grallaria guatimalensis* appears to be partial, including several inner greater coverts and several median coverts (Dickey & van Rossem 1938). Examination of specimens of five other *Grallaria* species (e.g., *G. squamigera*, *quitensis*, *bangsi*, and *rufficapilla*) indicate that the preformative molt is partial, with formative-plumaged individuals having retained outer greater coverts, primary coverts and a variable number of median and lesser coverts. In most cases, these juvenile coverts have buffy or rufous edging and distinctly contrast with the replaced coverts that lack edging. Likewise, the preformative molt in *Myrmothera* and *Pittasoma* is partial and does not include primary coverts, flight feathers, and, in some cases, several outer greater coverts (e.g., *Pittasoma michleri*). The extent and duration of juvenile and formative plumages across other taxa remains undocumented but could prove useful in age-class differentiation. No prealternate molt has been documented in this family.

Furnariidae (probably CBS and CAS). Many species appear to have distinct juvenile plumages, although documentation is lacking and plumage categorization may be difficult (Remsen 2003). Some genera may lack age-related differences (e.g., *Sclerurus*) (Howell & Webb 1995). Juvenile plumage in some *Furnariidae* is characterized by the reduction or absence of contrasting plumage patches found in definitive plumage, dusker feather margins in the throat and breast, and an ochraceous wash on the underparts (Remsen 2003). The duration of the juvenile plumage likely lasts from a few weeks to a few months (Howell & Webb 1995, Remsen 2003).

The extent of the preformative molt in furnariids is highly variable, with several genera (e.g., *Hyloctistes*, *Syndactyla*, *Philydor*, and *Automolus*) showing evidence of a complete

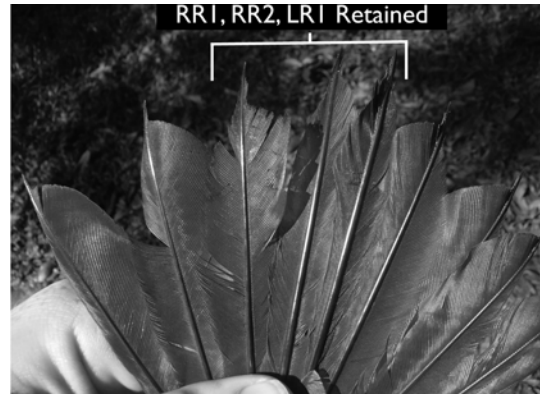


FIG. 3. The retention of central rectrices may be useful for age class differentiation in some species of Dendrocolaptids. *Dendrocolaptes certhia* is pictured here showing retained center rectrices.

preformative molt, whereas other genera (e.g., *Synallaxis*, and *Cranioleuca*) show substantial evidence of a partial preformative molt. Dickey & Van Rossem (1938) documented retention of rectrices and flight feathers in *Synallaxis* during the preformative molt. Our studies of specimens of eight other *Synallaxis* species (e.g., *S. ruficapilla*, *azarae*, *frontalis*, *obscura*, *cabanisi*, *spixi*, *hypospodia*, and *albescens*) and seven *Cranioleuca* species (e.g., *C. pyrrophia*, *erythroptis*, *curtata*, *suberista*, *vulpina*, *marcapatae*, and *albiceps*) revealed a partial preformative molt with retained rectrices, flight feathers, and alula feathers, which contrast with the replaced lesser and median coverts. The retention of greater coverts varies by genera, with *Synallaxis* species showing complete replacement and *Cranioleuca* species replacing zero to all greater coverts. These two genera both probably retain all primary coverts. Dickey & Van Rossem (1938) also documented an extensive definitive prealternate molt in *Synallaxis erythroptis* which includes some body feathers and (usually) complete rectrix replacement. Further field and museum information is needed for genera that appear to have complete preformative molts (see above). Molt timing, sequence, and overlap

with breeding remain poorly documented for the family (Renssen 2003), although a male *Synallaxis erythroptis* tending a nest in El Salvador was collected in extensive body molt, suggesting breeding-molt overlap in at least one species (Dickey & Van Rossem 1938).

Subfamily Dendrocolaptinae (CBS). The existence of a distinct juvenile plumage in most dendrocolaptids is undocumented. Many taxa may have a juvenile plumage that resembles a loosely textured definitive plumage, or have distinctly barred underparts, yet further documentation is required. Juvenile plumage in *Lepidocolaptes* closely resembles definitive plumage, although it may have darker and richer color overall and more prominent black edging to the streaking. The bill is dark colored, attaining its full degree of lighter color when several months old (Dickey & van Rossem 1938).

The extent of molt in this family is currently poorly known. Some species of woodcreepers undergo a single definitive prebasic molt which lasts four to six months (Marantz *et al.* 2003), while other species complete the definitive prebasic molt in two months (e.g.,

Lepidocolaptes souleyetii) (Dickey & van Rossem 1938). For some species, age class differentiation may be complicated by a complete preformative molt (e.g., *Dendrocincla*, *Sittasomus*, *Glyphorhynchus*, *Nasica*, *Dendrocolaptes*; Howell & Webb 1995), although *Dendrocolaptes certhia* in Central America can apparently retain two to three central rectrices (Fig. 3). Recent photographic evidence of *Xipborhynchus flavigaster* from El Salvador suggests a partial preformative molt, including retained greater coverts (Pyle, per. com.). Field evidence suggests that formative-plumaged *Xiphocolaptes* tend to have more buffy coloration. This criterion, combined with retained flight feathers (tapered, shorter, with more extensive rufous on the inner webs) (Dickey & van Rossem 1938) and retained greater coverts (Pyle, pers. com.), may facilitate accurate age categorization. However, the above characters, except for the tapered nature of retained flight feathers, were not found in museum specimens of two other *Xiphocolaptes* species (e.g., *X. promeropirhynchus*, and *major*). Tapered flight feathers may be the best way to age woodcreeper species that retain flight feathers during the preformative molt. Unlike *Xiphocolaptes flavigaster*, which replaces rectrices during the preformative molt, the preformative molt in *Lepidocolaptes souleyetii* does not include the center pair of rectrices, although flight feathers are replaced (Dickey & Van Rossem 1938). This very unique replacement pattern is similar to *Dendrocolaptes certhia* (see above) and may reflect true retention of juvenile rectrices or a ‘suspension limit’ derived from the retention of rectrices from a previous definitive prebasic molt.

Apparently no prealternate molt occurs in this family. Typically, woodcreepers molt after the breeding season, although the timing of molt and breeding season may overlap in *Dendrocolaptes*, *Lepidocolaptes*, and *Xipborhynchus* (Dickey & Van Rossem 1938, Foster 1975, Marantz *et al.* 2003).

Tyrannidae (CBS & CAS). Juvenile plumages are distinguishable from definitive plumages in many genera (e.g., *Colonia*, *Tyrannus*, *Platyrinchus*, *Tolmomyias*, *Lophotriccus*, *Capsiempis*, *Elaenia* (brown above), and *Leptopogon* (typically paler below). Juvenile plumages in *Myiarchus* are characterized by the presence of buffy or rufous-edged wing coverts that are distinguishable from the yellowish white coverts of definitive plumages. In several other genera the color and width of the edging of rufous on wing coverts can help distinguish juveniles from adults (e.g., *Legatus*, *Megarhynchus*, *Myiodynastes*, *Myiozetetes*, *Pitangus*, and *Terenotriccus*).

The preformative molt is partial in many genera (e.g., *Contopus*, *Empidonax*, *Sayornis*, *Megarynchus*, *Myiozetetes*, *Myiodynastes*, *Mionectes*, *Myiarchus*, *Lophotriccus*, *Oncostoma*, *Rhynchocychus*, *Legatus*, and *Tyrannus*) to complete in others (e.g., *Todirostrum*, *Tolmomyias*, *Tyrannus*, and *Camptostoma*) and highly variable across the family (Dickey & van Rossem 1938, Howell & Webb 1995, Pyle 1997, Pyle *et al.* 2004, Wolfe & Pyle unpubl.). The preformative molt replaces some, none or all of the primaries, secondaries and rectrices, but most or all of the primary coverts are usually retained (Pyle *et al.* 2004). The presence, extent, and/or coloration of wing bars on the coverts are useful criteria for differentiating formative from later plumages in many genera (e.g., *Contopus*, *Empidonax*, *Sayornis*, *Megarynchus*, *Myiozetetes*, *Myiodynastes*, *Legatus*, and *Tyrannus*) (Howell & Webb 1995)(see above).

Prealternate molts occur in many genera (e.g., *Pitangus*, *Empidonax*, *Pachyramphus*, *Platysaris*, and *Myiarchus*) yet are variable in nature, being partial in first-year birds of some species, to nearly complete in others (Dickey & van Rossem 1938, Lanyon 1975, Pyle 1997, Wolfe & Pyle unpubl.). The extent of these molts remains undocumented for many tropical species. Generally, many genera also show distinct and recognizable eye color variation

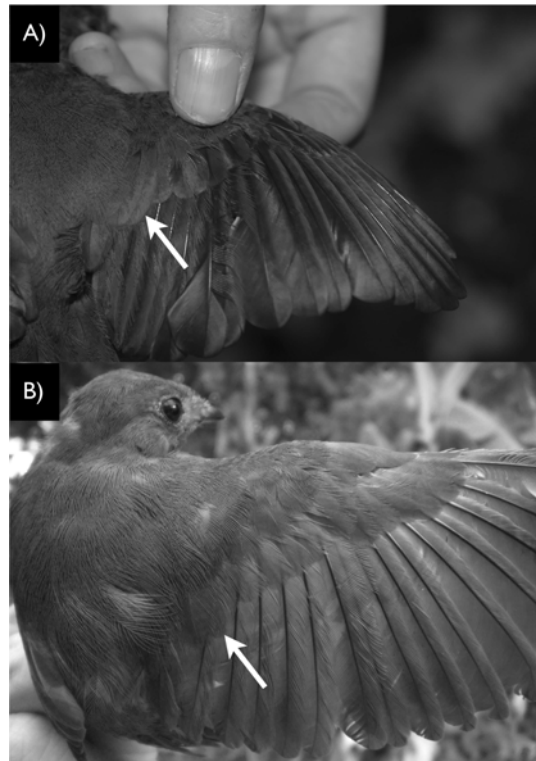


FIG. 4. Formative plumage in *Chiroxiphia pareola* (A) (photo: J. Blake) and formative plumage in *C. linearis* (B) with distinct molt-limits in the inner greater coverts designated with a white arrow. Note that retained juvenile coverts are shorter and more loosely textured than replaced feathers.

(e.g., *Oncostoma*, *Todirostrum*, *Tolmomyias*, and *Attila*; see Howell & Webb 1995 for detailed descriptions).

Pipridae (CBS). Molt in the family Pipridae is fairly well documented. The juvenile plumage is similar to female plumage in *Pipra*, *Machaeropterus*, *Chiroxiphia*, and *Manacus*, although it is likely duller in color and more loosely textured (Ryder, pers. obs.). Documentation of the juvenile plumage is still needed for *Neopelma*, *Xenopipo*, *Corapipo*, and *Masius* species.

The preformative molt is partial, where birds replace all body tracts and a variable number of greater coverts (Snow 2004) but

no rectrices, resulting in distinguishable molt limits (Ryder & Durães 2005, Doucet *et al.* 2007). Retained juvenile outer greater coverts in most manakin genera are shorter and more loosely textured than the replaced inner greater coverts (Fig. 4A & B) (also see figures in Ryder & Durães 2005). Consecutive molts are complete, and males within sexually dimorphic genera often reach definitive plumage during their second (*Manacus* species and *Pipra mentalis*), third (other *Pipra* species), fourth, and/or fifth (*Chiroxiphia* species) pre-basic molts (Foster 1987, McDonald 1993, DuVal 2005, Ryder & Durães 2005, Doucet *et al.* 2007). Many species in the genus *Pipra* also show variation in eye color with age (Ryder

pers. obs., Howell & Webb 1995). The single annual molt of manakins occurs at the end of the breeding seasons, although non-breeding males initiate molt before breeding females and adult males (Ryder unpubl.). No prealternate molt has been documented for this family.

Troglodytidae (CBS & rarely CAS). Some taxa show distinct juvenile plumages (e.g., *Thryothorus*, *Henicorbina*, *Microcerculus*, and *Campylorhynchus*) (Howell & Webb 1995, Kroodsma & Brewer 2005). The juvenile plumages in many other genera resemble the definitive plumage except for some subtle differences in coloration.

Little is known about the molt patterns of Central and South American wren species (Kroodsma & Brewer 2005). The preformative molt is typically partial (Howell & Webb 1995) and rarely incomplete. The preformative molt occurs within two or three months after fledging, where body feathers, and in some species, only a few flight feathers are replaced (Kroodsma & Brewer 2005). Based on both field observations and museum skins, the preformative molt in *Thryothorus nigricapillus* includes all wing coverts, usually the tertials and (occasionally) the central rectrices. Variability in the *Thryothorus* genera is evidenced by other species that only replace several inner greater coverts and sometimes one or more tertials, but no flight feathers or rectrices (Fig. 5). The replacement of flight feathers in some species during the preformative molt is often incomplete and eccentric, with southern populations of at least one species (e.g., *Thryomanes bewickii*) replacing more feathers than northern populations (Kroodsma & Brewer 2005). Therefore, other species with a broad latitudinal range (e.g., *Troglodytes aedon*) should be tested in order to reveal if this trend is more common among members of this family. Definitive prebasic molts are complete. At least one

tropical genus, *Cistothorus*, undergoes a partial prealternate molt before breeding, but this appears rare in the family (Kroodsma & Brewer 2005).

Turdidae (CBS & rarely CAS). Juvenile plumages of tropical *Turdus*, *Myadestes*, and *Catharus* are characterized by either buffy margins or spotting on the breast feathers and buffy shaft-streaking on back and covert feathers (Dickey & van Rossem 1938, Howell & Webb 1995).

Juvenile plumage is replaced by the preformative molt one to two months after fledging and is typically partial (Pyle *et al.* 2004). However, some tropical species may have incomplete (Pyle *et al.* 2004) or complete preformative molts (Howell & Webb 1995, Collar 2005). Age categorization is facilitated by retention of inner greater coverts, primary coverts, and rectrices. The second prebasic molt is typically complete (Pyle 1997). Much like temperate thrushes, most tropical species likely undergo one annual molt per year, but it is more protracted and may overlap with the reproductive cycle (Collar 2005). Prealternate molts are reported to occur in *Turdus infuscatus*; this prealternate molt includes body feathers and sometimes one or two rectrices (Dickey & van Rossem 1938). In addition, some species show variation in bill color with age (Howell & Webb 1995).

Thraupidae (CBS & CAS). Molt in tropical thraupid varies and is insufficiently known. Most species likely have juvenile plumages that are similar to definitive plumages but drabber in color and with more loosely textured feathers. Juvenile plumages have been observed in *Ramphocelus* and *Tangara* (D. Lebbin pers. com.), but the extent and duration of these plumages remains poorly documented (but see Mallet-Rodrigues *et al.* 1995). Many tropical tanagers attain a definitive plumage after the preformative molt. Data taken from



FIG. 5. Formative plumaged *Thryothorus rufalbus* with a molt-limit in the greater coverts and replaced tertials contrasting with retained secondary and primary flight feathers (photo: P. Pyle). Note the more extensive barring on the replaced greater coverts and tertials.

museums skins, however, suggest that some species of *Euphonia* have delayed plumage maturation, with males attaining a mottled appearance in second basic plumage. In addition, bill coloration maybe useful for aging species in at least two genera (e.g., *Habia*, and *Ramphocelus*).

Both field studies and evidence from museum specimens suggest that the preformative molt in many tropical tanagers is partial in nature (*Tangara*, *Dacnis*, *Tachyphonus*, *Chlorophonia*, *Piranga*, *Euphonia*, and *Thraupis*). A few genera appear to have complete preformative molts (*Buthraupis*, *Anisognathus*, and *Cyanerpes*), and some species within several genera possibly exhibit an incomplete preformative molts (*Ramphocelus*, and *Euphonia*). Extent of the preformative molt in most genera of tropical tanagers follows temperate patterns in which body plumage, lesser, median and a variable number of greater coverts are replaced, with rectrices, flight feathers and primary coverts retained. According to Dickey & van Rossem (1938) and Howell & Webb (1995), *Cyanerpes* has a complete preformative molt. Despite the complete nature of the preformative in *Cyanerpes*, accurate age

categorization is still possible, due to distinct preformative plumages (Dickey & van Rossem 1938). Some species of *Ramphocelus* (e.g., *R. nigrogularis*, and *passerini*) and *Euphonia* (e.g., *E. affinis*) have incomplete preformative molts where tertials and some primaries and secondaries are replaced. Nevertheless, these incomplete preformative molts are highly variable. Alternatively, *Ramphocelus bresilius* has been documented as having a complete preformative molt (Mallet-Rodrigues *et al.* 1995). *Euphonia* spp. show large amounts of variability both within and between species. In the genus *Piranga*, incomplete prealternate molts occur, which include some or all greater coverts and often the tertials and central rectrices (Dickey & van Rossem 1938, Pyle 1997). Other genera with documented partial prealternate molts are *Thraupis*, *Habia*, and *Cyanerpes* (Dickey & van Rossem 1938), but the existence of prealternate molts in most genera remains unknown. In all genera, the annual prebasic molt likely takes place after the breeding season.

Emberizidae (CAS & CBS). Streaky juvenile plumage is recognizable in many genera (for

Zonotrichia description see Miller 1961). The juvenile plumage in genera, such as *Atlapetes*, and *Aimophila*, can be characterized by having buffy-tipped greater coverts, a duskier and streakier breast and throat. *Sporophila* juvenile plumage is typically brownish overall with buffy-tipped greater coverts. *Oryzoborus* juvenile plumage is more loosely textured, yet resembles female and formative-plumaged individuals. *Arremon* typically has darker and browner flanks, and sooty breast and throat (Stiles & Skutch 1989).

After leaving the nest in juvenile plumage and prior to the preformative molt, at least one genus, *Passerina*, has a presupplemental molt comprised of only body plumage (Thompson & Leu 1995). Additionally, these presupplemental molts may also occur in *Aimophila* spp. (Pyle pers. com.). Preformative molts are variable, but generally partial to incomplete in extent, and in just a few genera, complete (e.g., *Arremonops* and *Volatinia*; Dickey & Van Rossem 1938, Miller 1961, Howell & Webb 1995, Wolfe & Pyle unpubl.). Although male *Volatinia* may have complete preformative molts, distinct delayed plumage maturation within the species is conducive to accurate age categorization (formative plumaged males are similar to females except for dark flight feathers and rectrices edged brown or gray; Dickey & van Rossem 1938, Howell & Webb 1995). *Saltator* species apparently retain rectrices and flight feathers during the preformative molt (Dickey & van Rossem 1938). Some *Oryzoborus* species have partial preformative molts which include body and some or all of the wing coverts, whereas the second prebasic molt in other members of this genus is incomplete or eccentric (e.g., *Oryzoborus funereus*).

Prealternate molts in the Emberizidae are sometimes absent (e.g., *Buarremon*, *Arremonops*, *Oryzoborus*, *Saltator*), partial (e.g., *Melospiza*, *Aimophila*, *Volatinia*, *Guiraca*, *Sporophila*, *Zonotrichia*, *Junco*, *Saltator*), or incomplete in other

genera (e.g., *Spizella*, *Aimophila*). Complex plumage sequences occur in the family; for example, Dickey & van Rossem (1938) stated that *Sporophila minuta* takes three years to reach definitive plumage. *Aimophila ruficauda* has been documented to have breeding-molt overlap (Dickey & van Rossem 1938).

Parulidae (CBS and CAS). Review of the literature and study of museum skins indicate that many genera (e.g., *Parula*, *Geothlypis*, *Myioborus*, *Basileuterus*, *Euthlypis*, and *Granatellus*) have distinct juvenile plumages (Curson *et al.* 1994). In many genera, juvenile plumages are characterized by buff, brown or rufous edging on the median and greater coverts forming two indistinct wing bars (e.g., *Parula*, *Myioborus*, *Euthlypis*, and *Basileuterus*) (for species specific details see Curson *et al.* 1994). Duller body and head plumage in relation to definitively-plumaged individuals may be apparent as well.

Preformative molts appear to be partial in most genera (e.g., *Geothlypis*, *Myioborus*, *Parula*, *Euthlypis*, and *Basileuterus*) and are partial or incomplete/complete in other genera (e.g., *Granatellus*). Typically, flight feathers, rectrices, primary coverts and a variable number of outer greater coverts are retained. These patterns result in molt-limits typically occurring in the outer greater coverts or between greater and primary coverts, with the retained juvenile feathers often showing distinct buffy or rufous tipping (Curson *et al.* 1994, Pyle pers. com.). Curson *et al.* (1994) document unclear patterns for *Granatellus*, in which *G. pelzelni* and *venustus* both show a partial preformative with retained flight feathers and rectrices while, *G. sallaei*, replaces tertials and outer secondaries. They assume the replacement of flight feathers suggests a complete molt but could also represent an incomplete preformative. A commonly used aging criterion for north temperate parulids that can be readily applied to their resident Neotropical counterparts is rectrix shape (see Pyle 1997).

The retained first-basic rectrices in many taxa are considerably more tapered than adult rectrices, which facilitates aging given experience with the species. Additionally, the amount of white in the outer rectrices of *Myioborus* and that of color in the crown of some species of *Basileuterus*, and *Myioborus* can help facilitate their age and sex categorization (Wolfe & Pyle unpubl. data). The existence of prealternate molts is not well documented in resident tropical parulids, but limited prealternate molts for certain species in *Geothlypis* and *Basileuterus* have been reported (Dickey & van Rossem 1938).

DISCUSSION

Here, we have compiled general information on molt strategy, plumage sequences, and extent of molt for 14 families and 1 subfamily of New World tropical landbirds. Our data on molt and plumage sequences collected for selected Neotropical avian families detail the existence of previously undocumented juvenile plumages and the extent of partial and incomplete preformative molts in a substantial number of genera. Of the 15 families treated, 11 showed distinct juvenile *vs.* adult plumages while four proved to be indistinguishable by plumage alone. We examined the extent of the preformative molt in 106 genera and found that 67 genera (63%) had partial preformative molt and 25 genera (24%) had incomplete preformative molts, providing distinguishable criteria useful for age categorization. The remaining 14 genera (13%) had complete preformative molts making age categorization difficult. Our review shows that the existence of prealternate molts is variable. Of the 15 families treated, ten lack a prealternate molt, three have a limited or partial prealternate molt, and two have an incomplete prealternate molt. The existence of prealternate molts in tropical taxa, however, requires further documentation. As such, we do not

rule out the possibility that documented prealternate molts might actually represent protracted preformative or prebasic molts. Overall, our results largely reflect patterns of plumage progression and molt extent in temperate zones.

Molt and plumage criteria facilitate accurate age classification in the vast majority of temperate landbird species (Jenni & Winkler 1994, Pyle 1997). Yet, research pertaining to molt of New World tropical residents has just begun receiving interest. In contrast, other attributes of avian life history are more often studied and, as a result, better represented in the contemporary ornithological literature. We believe this allocation to be disproportionate given the critical nature of molt in relation to the avian annual cycle (i.e., certain species may forgo migration and breeding events but no species has been documented forgoing the annual molt cycle). Recent work has shown that molt sequences in temperate passerines can provide a framework for understanding variation in patterns of feather replacement among tropical residents (Ryder & Durães 2005). Following the model presented here, further molt and plumage sequence documentation will inevitably facilitate the accurate age classification of tropical resident landbirds.

Our presentation is a review and a call for tropical ornithologists to begin collecting the molt data necessary to promote more detailed research into avian natural history and demographics. We have illustrated the potential for ornithologists to accurately age the majority of tropical residents via molt and plumage-based criteria. Complete preformative molts sometimes confound aging attempts in temperate latitudes in species, such as *Chamaea fasciata* and *Psaltriparus minimus*, and undoubtedly tropical ornithologists will face similar problems (e.g., subfamily, Dendrocolaptidae). However, given our current state of knowledge, complete preformative molts appear

rare in New World tropical taxa. The documented presence of delayed plumage maturation in several families (Pipridae, Rhinocryptidae, Thamophilidae) should facilitate accurate age classification for many species well into the second, third, and in some cases fourth molt cycle.

We do not claim that our data or presentation are exhaustive, but they rather provide a framework for further studies in the field as well as in museum collections. We believe this will facilitate and draw further interest to molt research at tropical latitudes. These data will ultimately enable us to place individuals into age classes, thereby enhancing our ability to model population demographics. Moreover, these models are essential for proactive population-level management. As tropical ornithology advances so must research on tropical molt patterns to begin building a robust age categorization framework for tropical taxa.

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