

2018

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Recommended Citation

Christensen, Tyler C. and Graesser, Sean P. (2018) "Molt and Ageing Criteria in Eight Birds from Northwestern Costa Rica," *North American Bird Bander*. Vol. 43 : Iss. 4 , Article 4.
Available at: <https://digitalcommons.usf.edu/nabb/vol43/iss4/4>

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Molt and Ageing Criteria in Eight Birds from Northwestern Costa Rica

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ABSTRACT

*Detailed descriptions of molt patterns and ageing techniques are lacking for many neotropical resident bird species. Using data collected from five years of December-January bird banding on the Nicoya Peninsula of the northwestern Pacific lowlands of Costa Rica, molt patterns and external ageing criteria were described for eight neotropical resident species frequently encountered in the region. Molt patterns and other ageing criteria observed in the species included in this study followed patterns regularly seen in North American species, but either have not been documented or are in conflict with existing literature. This study provides the first detailed accounts of molt patterns and other external age-deterministic characteristics in Black-headed Trogon (*Trogon melanocephalus*), Bright-rumped Attila (*Attila spadiceus*), Mangrove Vireo (*Vireo pallens*), Cabanis's Wren (*Cantorchilis modestus*), Long-billed Gnatwren (*Ramphocaenus melanurus*), and Gray-headed Tanager (*Eucometis penicillata*), and supplements existing literature describing molts of Rufous-and-white Wren (*Thryophilus rufalbus*) and Clay-colored Thrush (*Turdus grayi*).*

INTRODUCTION

Recognition of age-specific molt patterns are often the only reliable means for determining the ages of birds in the hand. Molt patterns and other ageing criteria are well-documented for much of the avifauna of North America and Europe (Dwight 1900, Jenni and Winkler 1994, Pyle 1997, Pyle 2008), and have proven useful in many studies of avian ecology and behavior (Desrochers 1992, Enstrom 1993, Ficken and Ficken 1967, Stutchbury 1994). While ageing methods have been utilized in some studies of neotropical bird

populations, ageing criteria for the majority of tropical bird species remain unknown, posing an obstacle for such research (Wolfe et al. 2010, Johnson and Wolfe 2018). Only recently have directed efforts been made to address this issue (see Johnson and Wolfe 2018).

Strategies of feather replacement tend to be similar between related Nearctic and Neotropical bird taxa (Wolfe et al. 2009, Johnson and Wolfe 2018). Although relatively few studies provide descriptions of specific molt patterns, much more is known regarding molt phenology in Neotropical birds. As in North America, molt in the Neotropics typically takes place separate from and immediately following reproduction (Marini and Durães 2001, Foster 1975). Breeding activity in most Costa Rican frugivorous and insectivorous species may occur from April-June (Skutch 1950).

To add to the body of knowledge of molt patterns and ageing criteria for resident Neotropical bird species, five years of detailed molt and plumage data, collected from November 2011--January 2016 during annual bird banding in western Costa Rica, were summarized. Data were collected by the authors and volunteers during annual operations of the Nicoya Peninsula Avian Research Station, a bird research and monitoring project with study sites along the eastern coast of the Nicoya Peninsula. Molt and ageing information was compiled for eight species of resident birds that are frequently encountered at these sites: Black-headed Trogon (*Trogon melanocephalus*), Bright-rumped Attila (*Attila spadiceus*), Mangrove Vireo (*Vireo pallens*), Rufous-and-White Wren (*Thryophilus rufalbus*), Cabanis's Wren (*Cantorchilis modestus*), Long-

billed Gnatwren (*Ramphocaenus melanurus*), Clay-colored Thrush (*Turdus grayi casius*), and Gray-headed Tanager (*Eucometis penicillata*).

METHODS

Banding sites were located at Refugio de Vida Silvestre Curu (9°47'18.69" N, 84°55'37.03" W) and Reserva Nacional Cabo Blanco (9°35'10.99" N, 85°5'50.27" W) on the eastern coast of the Nicoya Peninsula. Birds were captured using 12x 2.5m, 36mm mist nets. All Neotropical resident passerines and near-passerines received numbered aluminum leg bands allowing for individual identification upon recapture. Feathers were examined either by the naked eye or using a headset magnifier. Since little active molt took place during December and January banding, recognition of molt limits (contrasting feather "generations" resulting from partial and incomplete molts) was heavily relied upon to determine extents and sequences of molts. Molt limits were recognized by contrasting feather wear, barb density, color, or pattern between retained and replaced feathers (Rohwer and Manning 1990, Pyle 1997). Whenever possible, other age-related characters such as incomplete skull pneumatization, mouth color, and iris color were examined and used to corroborate age designations. When it was observed, active molt was determined by the presence of feather sheaths (Foster 1975).

The terminology used by Pyle (1997) to describe feather topography, molt extents (absent, limited, partial, incomplete, and complete), and sequences (typical, eccentric, and erratic) were followed, with the exception of our use of the term 'remiges', which we used when collectively referring to the primary and secondary flight feather tracts, and our use of the term 'secondary coverts' when referring to the greater coverts corresponding to the secondary flight feathers. Primaries are numbered from innermost (p1) to outermost (p9 or p10), secondaries from outermost (s1) to innermost (s6), and the tertials from innermost to outermost (t1-t3). Application of the familiar calendar-based age classification system used by Pyle to categorize ages of North American

birds was problematic, since reproduction of tropical species is not confined to a single nesting season as in temperate latitudes (Wolfe et. al. 2010). For this reason, all captured birds were assigned plumage classes based on their current feather coat, without assigning calendar-based age classes (Wolfe et. al. 2010). Molt cycle and plumage terminology defined by Humphrey and Parkes (1959) as updated by Howell et. al. (2003) was used.

The plumages of all captured birds were assigned to one of the following classes: juvenile, formative, first alternate, definitive basic, definitive alternate, unknown basic, unknown alternate, or unknown. For birds undergoing active molt or with visible molt limits, data sheets were used to record presence/absence of active body and flight feather molt, and to record the plumage to which each feather of the secondary and primary coverts, alula, tertials, secondaries, primaries, and rectrices belonged. Feather shape, especially of the distal feathers of a feather tract, was often useful in distinguishing feathers of juvenile and basic plumages. Data on the presence or absence of active flight feather or body molt was used to estimate the proportion of the population of each species undergoing active molt in December-January.

RESULTS

Of the species included in this study, only the Gray-headed Tanager showed evidence for a complete preformative molt. This species reached its definitive basic plumage after the preformative molt. The remaining species had a partial or incomplete preformative molt that resulted in a distinct formative plumage with recognizable molt limits; these species attained definitive basic plumage following the second prebasic molt. In most species, only a small proportion of individuals was actively molting. Those that were in active molt were mostly in the final stages of molt sequences. With the exception of Gray-headed Tanager, no juvenile plumages were observed. No species showed evidence of prealternate or inserted molts other than those mentioned.

SPECIES ACCOUNTS

Black-headed Trogon ($n = 45$): Active body molt was observed in nine individuals (20%). Active flight feather molt was observed in three individuals (7%). The preformative molt was partial and followed typical sequence, involving replacement of all body feathers, some to all lesser and median coverts, 0-7 inner secondary coverts, 0-3 alulae, 0-3 tertials, and 0-2 inner secondaries. The definitive prebasic molt appeared to be complete and followed the typical sequence, although occasionally 0-3 inner secondaries was retained from previous plumages. The formative plumage had body plumage resembling the definitive basic plumage, but the retained juvenile lesser, median, and secondary coverts, tertials, and inner secondaries were duller brownish-black and relatively worn, with bold white barring or edging. Retained juvenile outer secondaries, primaries, and primary coverts were also dull brownish-black and relatively worn, although they lacked white barring or edging. Replaced formative lesser, median, and secondary coverts, tertials, and inner secondaries were darker black and fresher than adjacent retained juvenile feathers, and were without white barring or edging. Juvenile outer rectrices (r5-r6) were distinctly narrower and more pointed than in definitive basic plumages, and had white barring. Definitive basic plumages were characterized by wing coverts, flight feathers, and outer rectrices that were uniformly black and lacked white barring or edging, and definitive basic outer rectrices (r5-r6) that were broader and more square-tipped than corresponding juvenile rectrices. Some inner secondaries were occasionally retained from previous basic plumages. The retention of recognizably juvenile secondaries in otherwise definitively-plumaged birds would indicate second-basic plumage, although this was not observed. Individuals were easily sexed in both formative and definitive plumages: males had iridescent blue-green backs, dark black heads, and iridescent blue-green dorsal surfaces of the central rectrices (r1); females had dull grayish-black heads and backs that lacked iridescence, and dull black dorsal surfaces of the central rectrices (r1).

Bright-rumped Attila ($n = 21$): Active body molt was not observed. Active flight feather molt was observed in three individuals (14%), all of which appeared to be in the final stages of flight feather replacement. The preformative molt was incomplete and eccentric, involving replacement of all body feathers, all lesser and median coverts, 2-6 inner secondary coverts, 2-3 tertials, 0-3 inner secondaries, 6-7 outer primaries, and possibly some to all rectrices. The definitive prebasic molt was complete and was suspected to follow the typical sequence based on observations of three actively molting birds. The formative plumage was superficially similar to the definitive basic plumage. Molt limits occurred among the secondary coverts, tertials, secondaries, and primaries. The base color and rachises of retained juvenile remiges was often recognizably lighter brown than the adjacent replaced formative remiges. Feathers of the definitive basic plumage were uniform in color, texture, and wear, and contained no noticeable molt limits. Iris color was found to be useful in ageing, ranging from light gray-brown to reddish-brown in first-cycle birds and from brownish-red to dark red in definitive-cycle birds.

Mangrove Vireo ($n = 21$): Active body molt was not observed. Active flight feather molt was observed in two individuals (9%), both of which appeared to be in the later stages of flight feather replacement. Based on molt limits, preformative molts were partial to incomplete, involving replacement of all body feathers and all lesser and median coverts, erratic replacement of 4 to all secondary coverts, 0-3 alulae, 2-3 tertials, inner 0-2 secondaries, and 0 to all rectrices. Definitive prebasic molts were complete. The formative plumage was superficially similar to the definitive basic plumage. Molt limits occurred among the secondary coverts, alulae, tertials, inner secondaries, and rectrices. Retained juvenile secondary coverts were slightly shorter, more coarsely-barbed, relatively worn and with less bold white tips, compared to the slightly longer, more densely-barbed, fresher and boldly white-tipped replaced formative secondary coverts. The definitive basic plumage was uniform in color,

texture, and wear, and contained no noticeable molt limits. Iris color appeared to vary markedly and may be indicative of age, but this was not confirmed.

Rufous-and-White Wren ($n = 70$): Active body molt was observed in four individuals (6%). Active flight feather molt was observed in nine individuals (13%), all of which appeared to be in the final stages of flight feather replacement. Based on molt limits, the preformative molt was incomplete and eccentric, involving the replacement of all body feathers and all lesser and median coverts, 2 to all inner secondary coverts, 0-3 alulae, occasionally some primary coverts, 2-3 tertials, 0-1 inner secondaries, 6-8 outer primaries, and all rectrices. The definitive prebasic molt was complete and appeared to follow the typical sequence based on observations of four actively molting birds. The formative plumage was superficially similar to the definitive basic plumage, but had molt limits among the secondary coverts, alulae, primary coverts, tertials, secondaries, and primaries. The base color and rachises of retained juvenile remiges were recognizably lighter brown than the adjacent replaced formative remiges. The black barring pattern on replaced formative remiges was bolder and more tightly-spaced. Wing and tail feathers of the definitive basic plumage were uniform in color, texture, and wear, and contained no noticeable molt limits. See Wolfe et al. (2009) and Ruíz-Sánchez et al. (2012).

Cabanis's Wren ($n = 9$): Active body molt was observed in two individuals (22%). Active flight feather molt was observed in four individuals (44%). The preformative molt was incomplete and eccentric, involving the replacement of all body feathers and all lesser and median coverts, 2-all inner secondary coverts, 0-2 alulae, 2-3 tertials, 0-2 inner secondaries, 5 to all outer primaries, and possibly all rectrices. The definitive prebasic molt was complete and followed typical sequence. The formative plumage was superficially similar to the definitive basic plumage. Molt limits occurred among the secondary coverts, alulae, tertials, secondaries, and primaries. Retained juvenile outer secondary coverts, when present, were more coarsely-barbed and relatively worn compared

to the more densely-barbed and fresher replaced formative inner secondary coverts. The base color and rachises of retained juvenile remiges were usually slightly lighter brown than the adjacent replaced formative remiges. Replaced basic remiges were darker and glossier, and had bolder black barring than the duller and less boldly-barred juvenile remiges. The definitive basic plumage was uniform in color, texture, and wear, and contained no noticeable molt limits.

Long-billed Gnatwren ($n = 9$): Active flight feather and body molt was observed in two individuals (22%). Based on molt limits, the preformative molt was partial, involving replacement of all body feathers and all lesser and median coverts and 3-6 inner secondary coverts. Definitive prebasic molts were complete and appeared to follow the typical sequence based on observations of two actively molting definitively-plumaged birds. The formative plumages were superficially similar to definitive basic plumages. Subtle molt limits occurred among the inner secondary coverts. Retained juvenile secondary coverts were slightly shorter, more coarsely barbed, and relatively worn compared to the slightly longer, more finely barbed, and fresher replaced formative secondary coverts. The definitive basic plumage was uniform in color, texture, and wear, and contained no noticeable molt limits.

Clay-colored Thrush ($n = 77$): The subspecies studied was *T. g. casius* (Carraker 1910). Active body molt was observed in nine individuals (12%). Active flight feather molt was observed in three individuals (4%). The preformative molt was partial and followed the typical sequence, involving the replacement of all body feathers and all lesser and median coverts, 0 to all inner secondary coverts, 1-2 alulae, 1-3 tertials, and occasionally the innermost secondary (s6) and innermost rectrices (r1-r2). Definitive prebasic molts were complete and followed the typical sequence. The formative plumage was superficially similar to the definitive basic plumage. Molt limits occurred among the secondary coverts, alulae, tertials, and occasionally the inner secondaries. The retained juvenile outer secondary coverts were usually shorter, more coarsely barbed, often had distinct

buff tips, and were relatively worn compared to the longer, more densely-barbed, untipped, and fresh replaced formative secondary coverts. Other retained juvenile feathers were lighter in color, more coarsely-barbed, and relatively worn. The definitive basic plumage was uniform in color, texture, and wear, and contained no noticeable molt limits.

Gray-headed Tanager ($n = 108$): The juvenile plumage was characterized by a uniformly olive-green head and upperparts and greenish-yellow underparts. Active body molt was observed in 20 individuals (19%). Active flight feather molt was observed in 27 individuals (25%). Based on observations of actively molting birds, the preformative molt was usually complete and followed the typical sequence, although occasionally ($n = 2$) 1-2 inner juvenile primary coverts were retained, allowing differentiation of the formative plumage from definitive basic plumages. The definitive prebasic molt was complete and followed the typical sequence. Iris color was found to be related to age, ranging from light gray-brown in juveniles to dark red in definitive-cycle adults. Most birds appeared to complete the preformative molt prior to iris maturation, so for a short window otherwise definitive-looking birds could be identified as in formative plumage by the presence of brownish-red irises. Adult birds had dark red irises and the definitive basic plumage was uniform in color, texture, and wear, and contained no noticeable molt limits.

DISCUSSION

The preformative molt of Rufous-and-white Wrens observed during this study was markedly more extensive than those described from individuals in Costa Rican highlands of the Cordillera de Tilarán (Wolfe et al. 2009), in which only partial molts were observed that involved replacement of the inner 3-6 secondary coverts, all tertials, and no remiges. Less extensive preformative molts were also reported in two other neotropical wren species, the Spot-breasted Wren (*Pheugopedius maculipectus*) and White-breasted Wood-Wren (*Henicorhina leucosticta*), in which replacement of a variable number of wing coverts,

alulae, and tertials but no primaries, secondaries, or rectrices was observed (Ruíz-Sánchez et al. 2012).

The preformative molt of Clay-colored Thrushes were only slightly more extensive, but otherwise similar to those described for the more northerly *T. g. tamaulipensis* (Pyle 1997), which included 2-10 secondary coverts and infrequently 1-2 tertials, but no rectrices.

Molt patterns of the species included in this study were similar to those known in related taxa of North America (see Pyle 1997). The infrequent observations of juveniles and birds in active molt in December and January are consistent with published information on typical breeding and molting phenology in the region (Skutch 1950, Foster 1975). This study treated species for which sufficient molt information could be gathered, and represents only a minority of the total species encountered. We suspect that many of the species in which no molt limits were observed possessed complete preformative molts, which would have resulted in formative plumages that were indistinguishable from subsequent plumages. Since the plumages of many neotropical species are sexually monomorphic, most species could not be sexed. Breeding season and post-breeding season data collection would provide more information on age and sex differences as well as molt and reproduction strategies of the birds of the region.

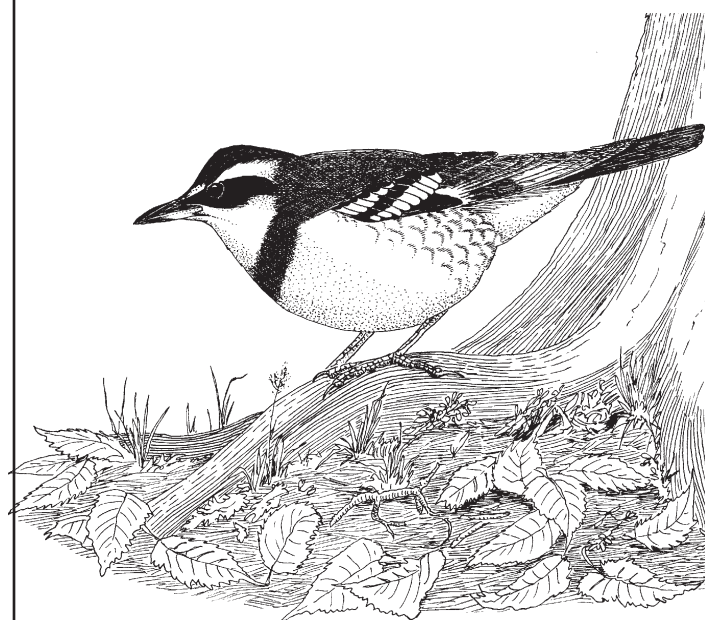
ACKNOWLEDGMENTS

This paper is happily dedicated to Hannah B. Suthers on the occasion of her 86th birthday, and to the 40th anniversary of her ongoing bird banding operation in the Sourland Mountain region of New Jersey. Hannah has been a source of friendship, inspiration, and advice for many years and to a great many people, and we thank her for her continued efforts. We also thank Peter Pyle, Walter Sakai, and Andrew Wiegardt for their thoughtful comments on our original manuscript.

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