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Examination of Macaulay Library images to determine avian molt strategies: A case study on hummingbirds

Peter Pyle¹

ABSTRACT—I examined images of over 6,300 individual hummingbirds from the Cornell Lab of Ornithology’s Macaulay Library to clarify conflicting reports on molt and plumage strategies in 8 species that breed or have bred primarily in the southwestern United States. Fixed replacement sequences from 2 nodes among primaries and 2 nodes among secondaries were found without exception, conforming to the findings of previous studies. I concluded that the preformative molt varied from limited to partial in 3 species, partial to incomplete in 3 species, partial to complete in 1 species, and complete in 1 species. Results of this study clarify molt terminology in Trochilidae as based on evolutionary homologies, and they establish new criteria for age determinations. The Macaulay Library clearly provides an important resource for the investigation of avian molts and plumages. I present a road map for such studies and suggest many other questions on avian molt that can also be investigated. I encourage contributors to the Macaulay Library to take and upload images of birds in molt or in worn plumages. *Received 18 January 2021. Accepted 7 December 2021.*

Key words: molt sequence, molt terminology, preformative molt, synapomorphy, Trochilidae.

Análisis de imágenes de la Macaulay Library para determinar las estrategias de muda de las aves: un estudio de caso sobre colibríes

RESUMEN (Spanish)—Analice imágenes de más de 6,300 individuos de colibríes de la Macaulay Library del Cornell Lab of Ornithology para clarificar reportes conflictivos estrategias de muda y plumaje en 8 especies que anidan o han anidado principalmente en el sureste de los Estados Unidos. Sin excepción, encontré secuencias fijas de reemplazo de 2 nodos entre primarias y 2 nodos entre secundarias, en concordancia con los hallazgos de diferentes estudios. Concluí que la muda preformativa varió de limitada a parcial en 3 especies, parcial a incompleta en 3 especies, parcial a completa en 1 especie y completa en 1 especie. Los resultados de este estudio clarifican la terminología de muda en Trochilidae como basada en homologías y establecen nuevos criterios para determinaciones de edad. La Macaulay Library claramente provee un recurso importante para la investigación de mudas y plumajes de aves. Aquí presento una hoja de ruta para dichos estudios y sugiero muchas otras preguntas sobre la muda de las aves que también pueden ser investigadas. Conmino a quienes contribuyen a la Macaulay Library a que tomen y envíen imágenes de aves en muda o en plumajes con desgaste.

Palabras clave: muda preformativa, secuencia de muda, sinapomorfía, terminología de muda, Trochilidae.

Our understanding of avian molt strategies has lagged behind that of other aspects of avian natural history (Bridge 2011, Marra et al. 2015), and this lack of knowledge is especially acute among the large number of bird species found in equatorial regions (Craig 1983, Mulyani et al. 2017, Johnson and Wolfe 2018). Although study of specimens has been instrumental in advancing our knowledge of avian molts, relatively few birds have been collected while undergoing active molt (Rohwer et al. 2005), and large sample sizes are often needed to fully document variation in timing, location, and extent of molts within a species’ annual cycle and throughout its geographic range. Furthermore, most specimens have been collected during the late 19th and early 20th centuries and may not reflect more recent changes of molt strategies (Kiat et al. 2019b).

Traditionally, hummingbirds in the United States and elsewhere were assumed to undergo

complete preformative and prebasic molts and to lack prealternate molts (Williamson 1956, Baltosser 1995, Pyle 1997, Howell 2002, Wolfe et al. 2009). However, the discovery of definitive prealternate molts in Ruby-throated (*Archilochus colubris*) and Rufous (*Selasphorus rufus*) hummingbirds has led to other proposed terminologies based on the evolution of molts in Apodidae (Dittmann and Cardiff 2009, Howell 2010, Sieburth and Pyle 2018, Weidensaul et al. 2020). With the exception of the presence or absence of prealternate molts, the strategies of the 8 species in genera *Archilochus*, *Calypte*, and *Selasphorus* that breed in the United States (hereafter “northern” hummingbirds) are reasonably well documented (Williamson 1956, Baltosser 1995, Pyle 1997, Pyle et al. 1997, Howell 2002, Williamson 2002). However, those of the 8 species of genera *Eugenes*, *Lampornis*, *Calothorax*, *Cyananthus*, *Basilinna*, *Leucolia*, *Saucerottia*, and *Amazilia* that breed or have bred primarily in Texas and the southwestern United States (hereafter “southwestern” species) are not as well known. Clarify-

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ing molt strategies in these 8 southwestern hummingbirds, especially regarding those in the first molt cycle, will help with the application of correct terminology and thereby increase our understanding of the evolution of molts in hummingbirds.

Previously, I (Pyle 1997) and other authors have investigated hummingbird molt by examining specimens and data from banding stations. For the 8 northern species, there have generally been adequate sample sizes to accurately assess molt strategies, including of specimens collected on winter grounds in Mexico (Pyle et al. 1997, Sieburth and Pyle 2018). However, for the 8 southwestern species, sample sizes of specimens have been insufficient to gain a full understanding of molt strategies. Currently there is conflicting information on timing and extents of molts in these species as presented by Pyle (1997), Howell (2002), Williamson (2002), the *Birds of the World* accounts (Billerman et al. 2020), and additional data collected from banding stations in the United States and Mexico (Wethington 2020).

Beginning in the mid-2000s, the advancement of digital technology has allowed detailed examination of feathers and feather tracts in images of birds, which in turn has been used to study molts and plumages (Pyle 2008a, Viera et al. 2017, Panter 2021). Since this time, the quantity of available online images has increased exponentially, expanding the potential to augment data on bird molt collected from specimens. The Cornell Lab of Ornithology's Macaulay Library catalogues audio and video recordings and images of birds and other wildlife for scientific research, education, and conservation (<https://ebird.org/media/catalog>). Most of the bird images catalogued at the library were contributed as part of eBird, a citizen science project allowing both birders and researchers to archive count data, images, and other media resulting from observations in the field (Sullivan et al. 2009). The Macaulay Library provides comprehensive search functions that allow viewing of digital images after applying various filters including those for location, year(s), and month(s) of observation, and images can be ordered by date of observation, date uploaded, or a quality rating from users. Currently there are >30 million images of >10,000 bird species in the Macaulay Library catalogue (M. Medler pers. comm.), typically representing images from

throughout a species' annual cycle, and thereby providing an additional resource to augment samples based on specimens and banding data.

I examined images archived at Macaulay Library to document and clarify inconsistent information on molts and plumages for the 8 southwestern hummingbird species. My goals included evaluating extent of the preformative molt (partial, incomplete, or complete), establishing timing for all molts and plumages, confirming sequence of flight-feather replacement, applying results to age and sex determination, and using results to clarify molt terminology and further our understanding of the evolution of molts in these and other hummingbirds. An important additional goal is to provide a case study for using the Macaulay Library to study avian molts and plumages on a global basis.

Methods

Species examined for this analysis were Rivoli's Hummingbird (*Eugenes fulgens*), Blue-throated Mountain-gem (*Lampornis clemenciae*), and Lucifer (*Calothorax lucifer*), Broad-billed (*Cyanthus latirostris*), White-eared (*Basilinna leucotis*), Violet-crowned (*Leucolia violiceps*), Berylline (*Saucerottia beryllina*), and Buff-bellied (*Amazilia yucatanensis*) hummingbirds. I sought to assess molt patterns within populations of these species that breed or occur north of Mexico. Therefore, I set eBird's location filter of Macaulay Library images to the United States. For each species I used the month filter to examine images for each month of the year. For Lucifer, White-eared, and Berylline hummingbirds, I concluded that sample sizes of images from the United States year-round were insufficient to gain an accurate assessment of molt patterns (e.g., <10 images taken during some winter months). I therefore set the filter to Mexico and augmented the sample by examining images taken in Mexican states bordering the United States and those on the Central Mexican Plateau south to Mexico City, with the assumption that these bioregions included wintering individuals from the United States or breeding populations that exhibited similar molt strategies (Howell 2002). Within each month I ordered the images by date, from oldest to newest. This allowed better tracking of individual hummingbirds, for example, vagrants

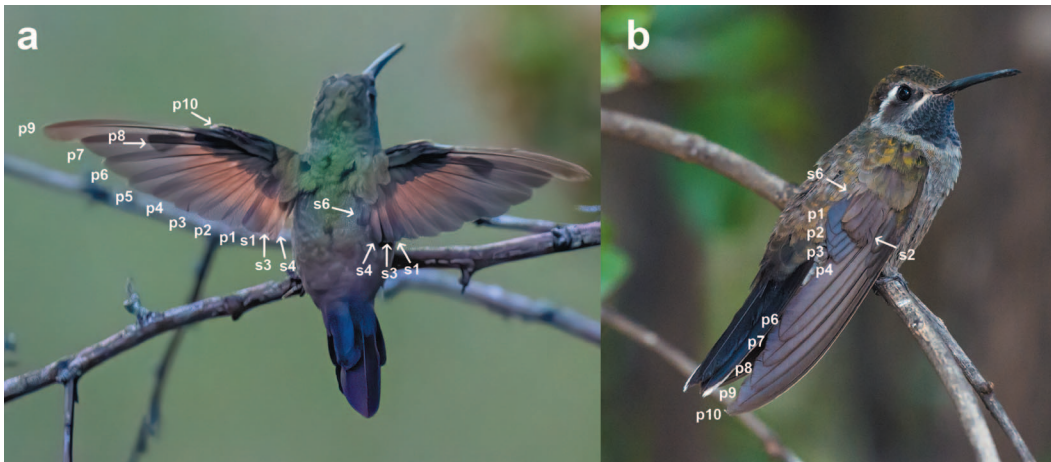


Figure 1. Examples of primary and secondary numbering and replacement sequences in hummingbirds. (a) Berylline Hummingbird (*Saucerottia beryllina*), 17 May 2020; and (b) Blue-throated Mountain-gem (*Lampornis clemenciae*), 9 Aug 2018. Sequence was determined by identifying newly replaced vs. unmolted feathers and assessing the lengths of growing feathers. In hummingbirds, primaries molt distally from a node at p1 and proximally from a node at p10, with p9 the last feather replaced, and secondaries molt proximally from a node at s6 and distally from a node at s1, with s4 usually the last feather replaced. Note that p10, s2, and s5 in (a) and p5 and s1 in (b) have dropped and are not visible; note also the “molt clines” in (b), with p9 the newest (latest replaced) primary and s4 the newest secondary, signaling a previous complete molt, which can assist with plumage (age) determination (Supplemental Fig. S1–S9). Photos cropped for enlarged presentation and used by license agreement from the Macaulay Library © Mel Senac (a, ML238319331) and Suzie McCann (b, ML116501471).

or those of rarely occurring species at popular feeding stations, thereby minimizing duplication of data from the same individuals.

For each of these 8 species, I reviewed all images at the Macaulay Library from these areas that were uploaded through July 2020. Hummingbirds that I concluded were misidentified to species (<1%) were excluded. Data were recorded only from images that could be properly assessed for both plumage (age) and molt status; e.g., all primaries of the wing were visible or accounted for in molt (Fig. 1). In many cases, the eBird checklist contained multiple images of the same individual, which helped with accurate determinations. Individuals that were not confidently aged were excluded. For data summaries I also excluded images of the same individual within a month as conservatively as possible based on eBird checklist data (see Supplemental Table S1 for numbers of images excluded): a bird of similar molt and plumage status (see below) within 7 d of a previous observation at the same location was assumed to be the same individual. Individuals with images that spanned months were recorded for each month of occurrence.

For each individual, I determined plumage (including molt cycle or age) and molt status. Plumages in both males and females were identified following the ageing criteria of Pyle (1997), Howell (2002), and Williamson (2002), along with new criteria presented here (Supplemental Fig. S1–S9). Criteria based on wing feathers, rectrices, and for some species bill color, were emphasized. Criteria related to the iridescent feathering in males was evaluated with caution due to effects of lighting on the perceived coloration of these feathers in digital images. Extent of corrugation at the base of the culmen (Ortiz-Crespo 1972, Pyle 1997, Yanega et al. 1997) was also examined but could only be evaluated on a small proportion of images.

For individuals in active molt, replacement sequence of primaries, secondaries, and rectrices was assessed (Fig. 1). Primaries were numbered distally from p1 (inner) to p10 (outer) and secondaries proximally, from s1 (outer) to s6 (inner). Sequence was determined by identifying newly replaced vs. unmolted feathers and assessing the lengths of growing feathers. Examination of primary spacing (morphology) in birds not in

active molt was used on a comparative basis to determine precise sequences in molting birds, and symmetry among new, molting, and old feathers within both wings was confirmed, when possible, to ensure that missing and growing feathers reflected molt. Arrested or suspended molts among flight feathers (cf. Pyle et al. 1997) were noted as contrastingly new feathers in sequence among older unreplaced feathers on birds that were not in active molt (all remiges fully grown). Molt and molt limits among body feathers and upperwing secondary coverts were also assessed by evaluating pin and growing feathers along with contrasts between new and old feather generations. See the Supplemental Materials file for more detail on determining molts and plumages.

I categorized each individual into 1 of 6 plumage or molt states: (1) juvenile plumage (prior to evidence of preformative molt), (2) undergoing preformative molt, (3) formative plumage of body or flight feathers, (4) undergoing second prebasic molt of flight feathers, (5) definitive basic plumage, and (6) undergoing definitive prebasic molt of flight feathers. Partial preformative molts of body feathers are often protracted and/or suspended resulting in less-precise assignment of preformative molt or formative plumage. To more accurately separate birds undergoing preformative molt from birds considered to be in formative plumage, I looked for pin and growing feathers and also assessed when development of definitive-like appearance in males appeared to culminate within the entire sample of first-cycle males, including long-staying individuals (e.g., vagrant individuals at feeders) tracked while undergoing and completing preformative molt. Timing of molts and plumages in hummingbirds, except for gorget-feather replacement in males, shows little variation by sex (Williamson 1956, Pyle et al. 1997, Sieburth and Pyle 2018), and this also accorded with exploratory examination of Macaulay Library data for this study. Therefore, counts included both sexes combined. Images of interest are referenced by their Macaulay Library identifiers (“ML” followed by 8 or 9 numerals) and in some cases eBird Checklist identifiers (“S” followed by 7 or 8 numerals) when multiple images of the same bird documented the point of reference.

Results

A total of 27,581 images of the 8 southwestern hummingbirds from the Macaulay Library was examined for this study (Supplemental Table S1). These included 6,345 individuals from images that were of sufficient quality to assess plumage (age) and molt status and once duplicate images of the same birds were excluded. Total individuals by species ranged from 280 White-eared Hummingbirds to 2,413 Broad-billed Hummingbirds, totals by month ranged from 248 individuals for February to 1,245 for August, and totals by species in a month ranged from 4 Lucifer Hummingbirds in February to 639 Broad-billed Hummingbirds in July (Supplemental Table S1). Samples of >25 individuals were recorded for 75% of the months by species.

Sequence of feather replacement among primaries consistently proceeded distally from p1 to p8 followed by p10 and concluding with p9 (Fig. 1). Among images of 1,373 individuals recorded undergoing active primary molt, no exceptions to this sequence were observed (cf. Supplemental Fig. S1–S8), including among >10 known individuals that could be tracked for all or large portions of the molting period. The 6 secondaries of these species began to be replaced when p6 had dropped (e.g., ML181183661, ML46645931, ML122879681). Among 71 individuals in which active secondary molt could be evaluated, replacement invariably proceeded proximally from the innermost feather, s6, and distally from the outermost feather, s1 (Fig. 1). The orders in which s1 vs. s6, and s2 or s3 vs. s5 were molted were variable, but s4 was always the last feather to be replaced, near to or following completion of primary molt (e.g., ML195887161, ML34535671, ML100323371, ML33989911). Sequence of rectrix replacement was more difficult to evaluate in images but typically began with the central rectrices when p7 or p8 were dropped (e.g., ML184013981, ML188765281, ML34654481), after which replacement of remaining rectrices generally proceeded rapidly and distally (e.g., ML238319331, S56405130), with the outermost (r5) often replaced before r4 and/or r3 (e.g., ML238400031).

Suspended or arrested molts among non-molting remiges were rare, being recorded in only 23 individuals (<0.1% of 3,652 non-molting hummingbirds) of 6 species: Rivoli’s Humming-

bird, Blue-throated Mountain-gem, and Broad-billed, White-eared, Violet-crowned, and Buff-bellied hummingbirds. These were recorded during both preformative molts (see below) and definitive prebasic molts (e.g., ML45716111, ML212853441, ML86250771, ML51351041, S41676864), including individuals that had replaced all remiges except for the s4 (e.g., ML48860261, ML42333141, S2611244). Molts were suspended or arrested at a single feather-tract location within the above sequences, with the exception of one Buff-bellied Hummingbird that had suspended molt after replacing p1 and p6 most recently (ML22821451), perhaps following an earlier arrested molt. For the purposes of this study these birds were assumed to have arrested rather than suspended prebasic or preformative molts, which were thus assumed to be incomplete; many of these individuals were recorded late within the molt cycle, supporting this assumption. No retained rectrices resulting from suspended or arrested molts were noted but these could easily have been missed.

Sample sizes for the 6 molt and plumage categories, by month, for the 8 species are given in Supplemental Table S1. Dates for juveniles ranged from 2 February in Buff-bellied Hummingbird to 18 November in Berylline Hummingbird, and temporal duration periods for recorded juveniles ranged from 78 d in Violet-crowned Hummingbird to 184 d in Rivoli's Hummingbird (Supplemental Table S2). The preformative molt of body feathers was first detected from 9 d (in Berylline Hummingbird) to 80 d (in White-eared Hummingbird) following the earliest juveniles recorded in the spring. The temporal period between first detection of body-feather replacement to first detection of primary replacement varied from 0 to 1 months in White-eared and some Broad-billed Hummingbirds, to 6 months in Lucifer Hummingbird, 7–8 months in Berylline and Buff-bellied hummingbirds, 8–9 months in Violet-crowned Hummingbird, and 10–11 months in Rivoli's Hummingbird, Blue-throated Mountain-gem, and some Broad-billed Hummingbirds. Temporal periods for the preformative molt among populations ranged from about 4–5 months in White-eared Hummingbird, Lucifer Hummingbird, and Berylline Hummingbird, to 6–7 months in Blue-throated Mountain-gem and Violet-crowned Hummingbird, to 8–9 months in Broad-billed

Hummingbird, and 9–10 months in Rivoli's and Buff-bellied hummingbirds (Fig. 2, Supplemental Table S2).

I concluded that the preformative molt ranged from limited to partial in 3 species: Lucifer, Berylline, and Buff-bellied hummingbirds (Fig. 3, Supplemental Fig. S3, S7, and S8). These species replaced variable amounts of body feathers and upperwing secondary coverts, from a few body feathers only to most or all body feathers and secondary coverts, but replaced no primaries, primary coverts, secondaries, or rectrices until commencement of the second prebasic molt. Most Rivoli's Hummingbirds, Blue-throated Mountain-gems, and Violet-crowned Hummingbirds also underwent partial preformative molts (Fig. 1, Supplemental Fig. S1, S2, and S6), although small proportions, 1 of 126 first-cycle Rivoli's Hummingbirds in October–August (0.8%), 1 of 95 first-cycle Blue-throated Mountain-gems in November–August (1.1%), and 3 of 140 first-cycle Violet-crowned Hummingbird in August–May (2.1%), were replacing or had replaced 2–6 inner primaries during what I judged to be incomplete preformative molts (Fig. 4).

For White-eared Hummingbird I concluded that the preformative molt was complete. It was the only 1 of the 8 species in which timing of preformative and later molts was similar, the replacement of primaries commencing at the same time or even before juvenile body feathers began molting (Supplemental Fig. S5; ML252080431, S11291169) and completing following body-feather replacement, at which time males had acquired definitive-like appearance (Fig. 1 and 2, Supplemental Fig. S5). It was also the only species in which no males following the preformative or prebasic molt showed predefinitive appearance ($n = 64$). The longer period for juveniles recorded for this species (80 d) than the others (10–57 d) may also relate to the complete molt, juvenile flight feathers not needing to last for 5 months or more. As a result of this complete preformative molt, White-eared Hummingbirds in formative vs. definitive basic plumage and undergoing the second vs. definitive prebasic molts could not be distinguished in images for this study, with the exception of some birds in formative plumage with duller red bill colors than are found in older birds.

For Broad-billed Hummingbird, I concluded that the preformative molt varied from partial to

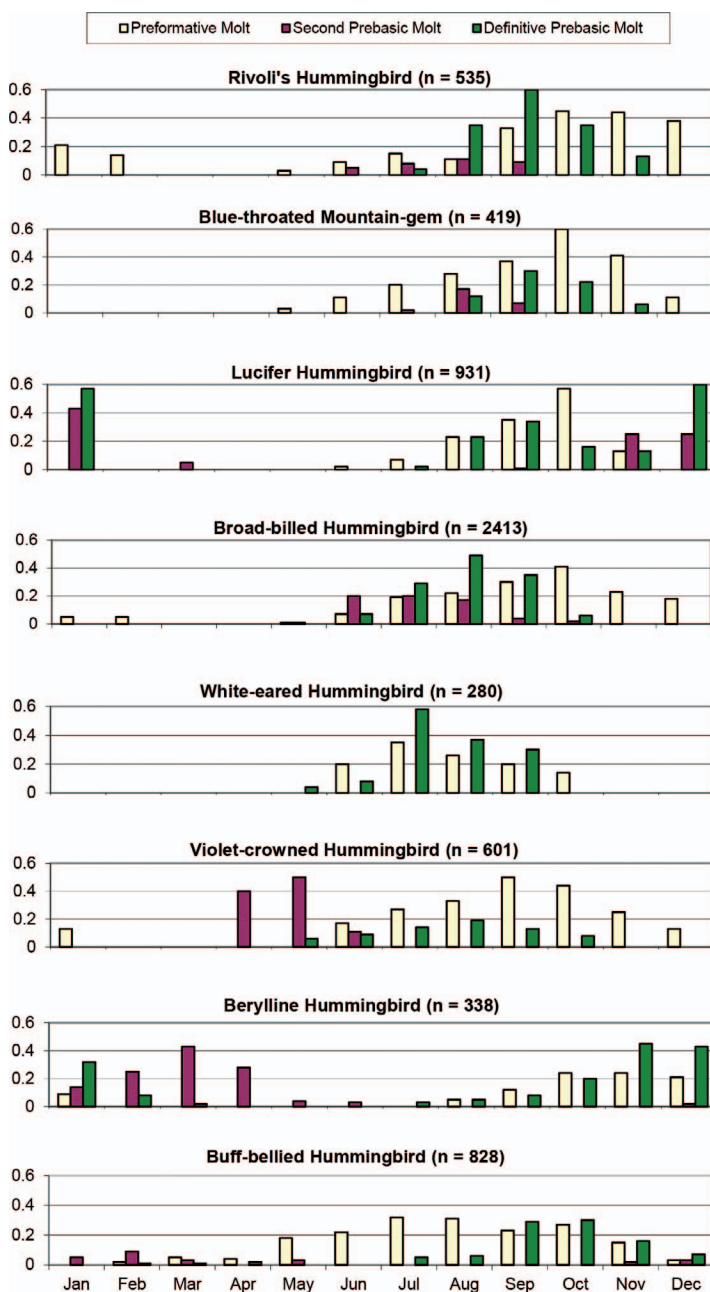


Figure 2. The timing of molt in 8 species of hummingbirds that breed in the southwestern United States. Bars represent proportion of the entire monthly sample that were undergoing each molt; see Supplemental Table S1 for specific sample sizes for each species by month.

complete (Fig. 2 and 3, Supplemental Fig. S4). Active molting of primaries and rectrices during the preformative molt of this species ($n = 29$) was recorded from 3 August (ML86966331) to 25

January (S33932855), with active molting of secondaries recorded through 16 February (ML208941611). For birds with incomplete or complete preformative molts, initiation of primary

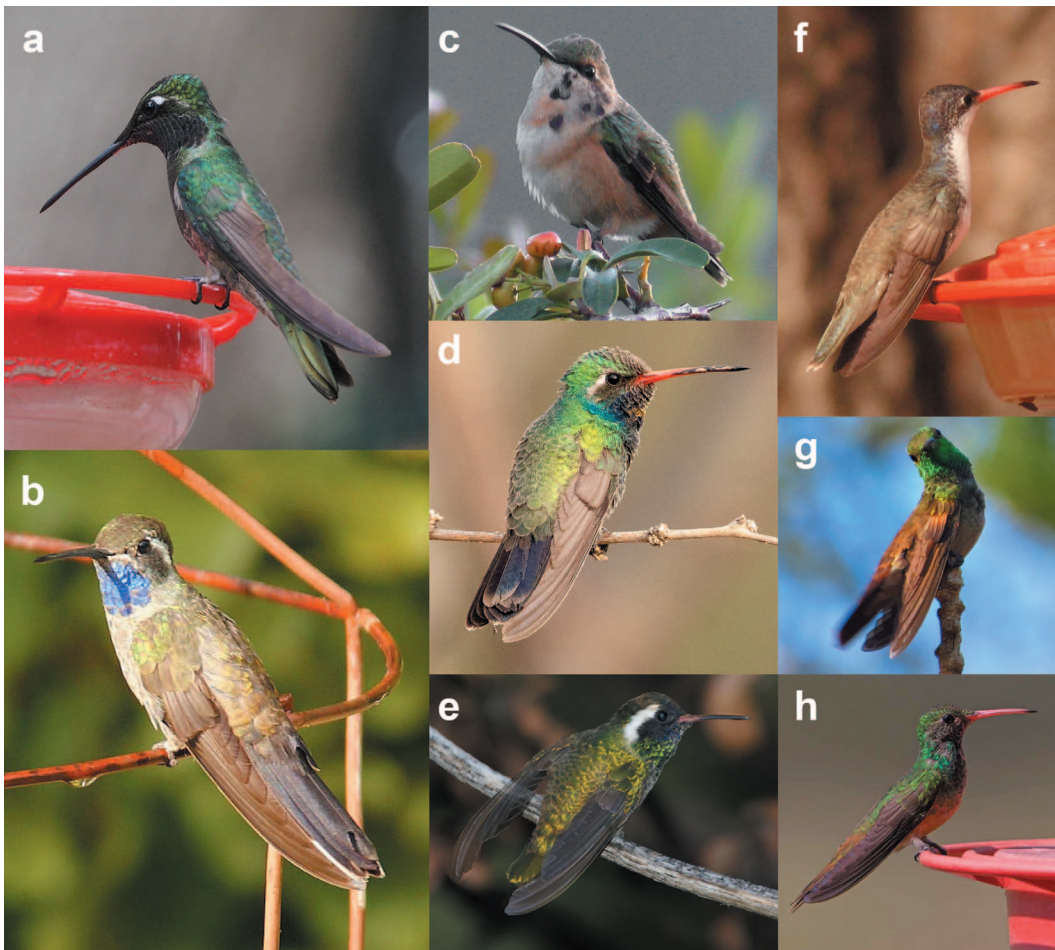


Figure 3. Examples of formative plumage in 8 species of hummingbirds that breed in the southwestern United States. (a) Rivoli's Hummingbird (*Eugenes fulgens*), 4 Aug 2019; (b) Blue-throated Mountain-gem (*Lampornis clemenciae*), 4 Aug 2012; (c) Lucifer Hummingbird (*Calothorax lucifer*), 5 Oct 2009; (d) Broad-billed Hummingbird (*Cyanthus latirostris*), 2 May 2019; (e) White-eared Hummingbird (*Basilinna leucotis*), 5 Aug 2008; (f) Violet-crowned Hummingbird (*Leucolia violiceps*), 6 Mar 2016; (g) Berylline Hummingbird (*Saucerottia beryllina*), 11 Feb 2017; and (h) Buff-bellied Hummingbird (*Amazilia yucatanensis*), 26 Apr 2017. Except for White-eared Hummingbird, note the retained juvenile primaries, worn brown secondaries, and molt limits among upperwing secondary coverts in most or all images. The White-eared Hummingbird (e) is finalizing a complete preformative molt (aged by dull bill color) after which formative plumage resembles definitive basic plumage in appearance. Photos cropped for enlarged presentation and used by license agreement from the Macaulay Library © Gjon Hazard (a, ML171639201), Ken Murphy (b, ML53554351), Ed Thomas (c, ML168356961), Philip Kline (d, ML156749041), Bill Hubick (e, ML188765291), Debby Parker (f, ML25520031), William Proebsting (g, ML49162901), and Joshua Covill (h, ML56665951).

replacement occurred within 0–1 months of initiation of body-feather replacement, as in White-eared Hummingbird, and for those with partial preformative molts, initiation of primary replacement occurred 10–11 months following initiation of body-feather replacement, as in Rivoli's Hummingbird and Blue-throated Moun-

tain-gem; few or no individuals appeared to commence molt of primaries within 2–9 months of body feather molt. In November–December, 56% of 32 first-cycle Broad-billed Hummingbirds were molting or had molted primaries, and in December–May at least 10 of 222 first-cycle individuals (4.5%) had suspended or arrested

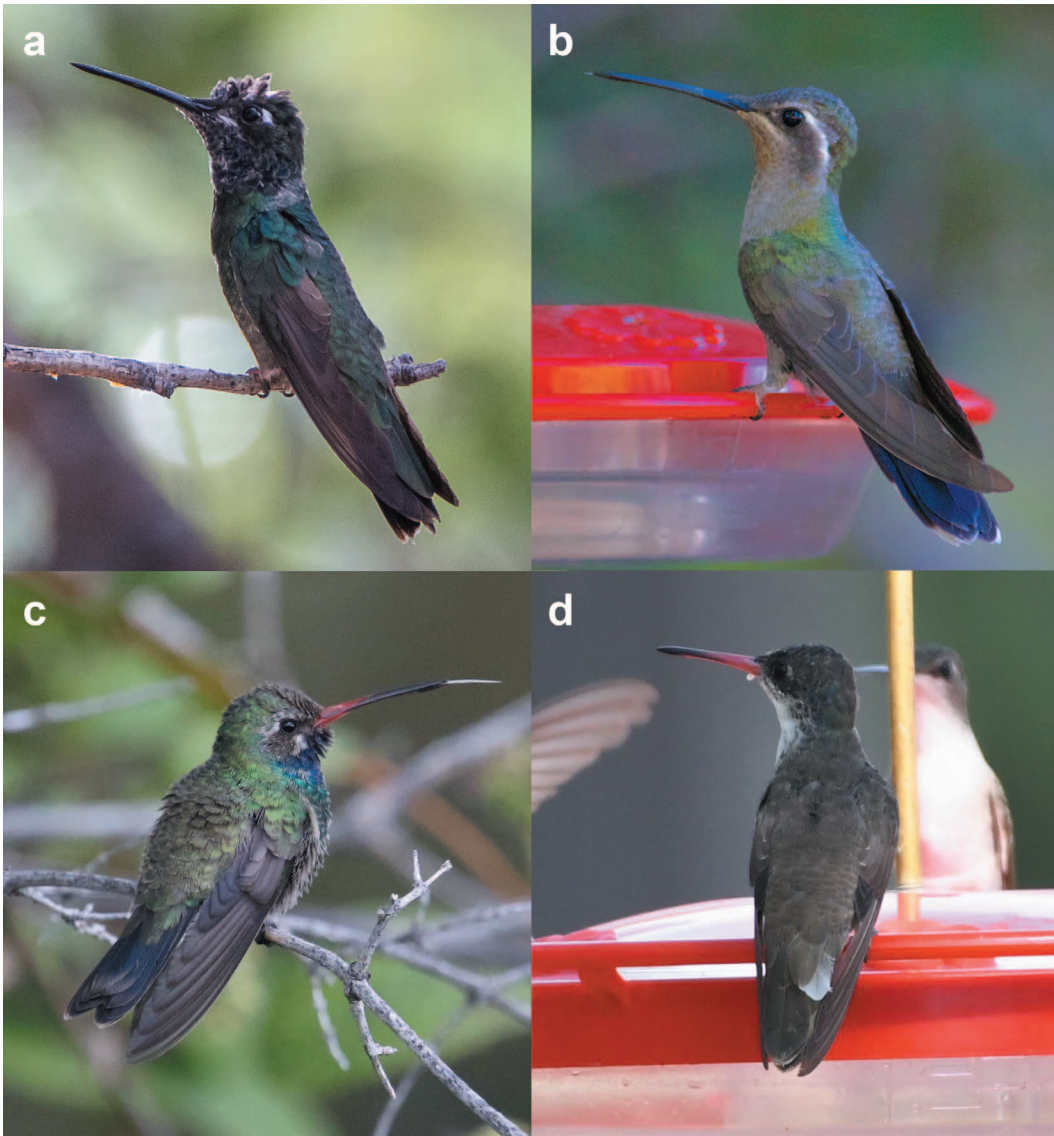


Figure 4. Incomplete (presumed arrested; see text) preformative molts in 4 species of hummingbirds that breed in the southwestern United States. (a) Rivoli's Hummingbird (*Eugenes fulgens*), 26 May 2018, having replaced p1–p3; (b) Blue-throated Mountain-gem (*Lampornis clemenciae*), 4 Aug 2012 having replaced p1–p4; (c) Broad-billed Hummingbird (*Cyananthus latirostris*), 16 September 2019, having replaced p1–p4; and (d) Violet-crowned Hummingbird (*Leucolia violiceps*), 31 Aug 2019 replacing p1–p6. Photos cropped for enlarged presentation and used by license agreement from the Macaulay Library © Lydie Mason Warner (a, S46054488), Gordon Atkins (b, ML101073691), Russ Morgan (c, S59856736), and Max Leibowitz (d, S59412857).

primary molt, most often at p2 (e.g., ML77579011) or p4 (Fig. 4; see also, e.g., ML47852161, ML22932271). Some males underwent a complete preformative molt of flight feathers but did not acquire definitive appearance

of body plumage whereas others acquired complete or near-complete definitive appearance in body feathering but retained juvenile flight feathers (Fig. 2, Supplemental Fig. S4 and S9). Some Broad-billed Hummingbirds following com-

plete molts likely become indistinguishable from individuals in definitive basic plumage and were categorized as in definitive basic plumage here.

Formative plumage in males (and in some cases females) of these 7 species, as aged by flight-feather characteristics, generally did not reach definitive appearance of body feathering, varying from showing no or a few iridescent display feathers in male Lucifer Hummingbirds to showing nearly full to full definitive appearance in male Broad-billed and male and female Berylline and Buff-bellied hummingbirds (Fig. 2, Supplemental Fig. S1–S4 and S6–S9). Formative plumages in male Rivoli's Hummingbird and Blue-throated Mountain-gem, and in both sexes of Violet-crowned and Buff-bellied hummingbirds, were variable and intermediate but few or no birds in formative plumage appeared to have acquired definitive appearance of body feathering (Supplemental Fig. S1, S2, S6, and S9). By contrast, definitive basic males of all 8 species (as aged by flight-feather characteristics) showed full definitive appearance, with the exception of a small proportion of Rivoli's Hummingbirds that had small and variable amounts of brown feathering in the lower breast; further study is needed on whether or not this may represent second basic plumage.

Within species, the temporal duration period for the second prebasic molt ranged from 63 d in Blue-throated Mountain-gem and 65 d in Violet-crowned Hummingbird to 188 d in Buff-bellied Hummingbird, and for the definitive prebasic molt duration ranged from 94 d in Blue-throated Mountain-gem to 271 d in Buff-bellied Hummingbird (Supplemental Table S2). With the exception of Buff-bellied Hummingbird the seasonal timing for these molts was well defined (Fig. 2, Supplemental Table S2). Known individual hummingbirds take less time within these periods to molt; e.g., a Berylline Hummingbird in Arizona in 2020 was documented completing a definitive prebasic molt in 49 d, from dropping p1–p3 on 26 April (S67876574) to completing growth of p9 and s4 on 14 June (ML244918451), and a Buff-bellied Hummingbird in Florida that had dropped inner primaries on 4 November 2016 (ML39279451) was completing molt 69 d later on 28 January 2017 (ML46926141). Within populations, timing of the second prebasic molt differed but overlapped that of the definitive prebasic molt in all 7

species, the overlap being earlier than the definitive prebasic molt in Rivoli's Hummingbird, Blue-throated Mountain-gem, Broad-billed Hummingbird, and Violet-crowned Hummingbird, and later than the definitive prebasic molt in Lucifer, Berylline, and Buff-bellied hummingbirds (Fig. 2). Based on my conclusions on the evolution of these molts, however, the second prebasic molt occurred earlier in timing than the definitive prebasic molt in all 7 species (see Discussion).

Discussion

Replacement sequences among remiges

Sequence of primary molt in hummingbirds has previously been reported as distal from a node at p1 and proximal from a node at p10, with p9 the last feather replaced (Wagner 1955, Williamson 1956, Stiles 1995, Pyle 1997, Howell 2002). This sequence was confirmed without exception among 1,373 molting hummingbirds of all 8 species in this study. Results of my study also indicate replacement nodes among secondaries to be fixed, with proximal replacement from s1 and distal replacement from s6 resulting in s4 being the last secondary replaced, without exception within my sample, including for Lucifer Hummingbirds (e.g., ML79210961), contradicting reports by Wagner (1955) of replacement from nodes in the center of the tract (see also Stiles 1995). These replacement nodes and directions among remiges are consistent with those found by Williamson (1956) for Anna's Hummingbird (*Calypte anna*) and by Stiles (1995) for 13 hummingbird species in Costa Rica, although Stiles also found that the last secondary replaced was s3 or s5 rather than s4 in a small proportion (6.2%) of 242 individuals in his study. My results on rectrix sequence are also consistent with those of Stiles (1995).

Unlike timing, location, and extent of molts, sequential replacement of remiges in birds appears to be very fixed (Pyle 2013), in which case I predict that these 4 remigial nodes and replacement directions will be found in all hummingbird species. Precise sequence among replacement waves (e.g., in hummingbirds, initiation at either s1 or s6 or order of s2 or s3 vs. s5) and terminal feathers where waves converge appears to be less fixed, evolutionarily, and may vary in birds according to wing physiology, flight requirements, or other parameters. The p9 is the longest primary

in hummingbirds and it has been proposed that its replacement follows that of p10 to maintain wing integrity in a bird family that relies heavily on flight for existence (Greenewalt 1975, Stiles 1995). A similar sequence among primaries in family Ardeidae (Shugart and Rohwer 1996, Pyle 2008b) has evolved independently, perhaps as driven by different constraints.

Timing and extent of the preformative molt

Additional results of this study otherwise clarify molt strategies in these 8 southwestern hummingbirds to a substantial degree. For example, preformative molts in 7 species are here interpreted to be partial in most individuals, differing from previous interpretations that they were complete (Pyle 1997, Howell 2002). In 3 of these species, Rivoli's Hummingbird, Blue-throated Mountain-gem, and Broad-billed Hummingbird, juvenile primaries can be retained for close to a year, consistent with strategies in most other birds with partial preformative molts (Howell et al. 2003; Pyle 1997, 2008b; Jenni and Winkler 2020) and with other species of *Lampornis* (Newell et al. 2007). Lucifer, Berylline, and Buff-bellied hummingbirds have molts more similar to northern North American species, in which body feathers are partially replaced during a preformative molt occurring 6–7 months before primaries are replaced as part of the second prebasic molt (see below). The timing of the second prebasic molt of Violet-crowned Hummingbird appears to be intermediate between these 2 groups and indicates that they may not breed in their first spring, although its apparently short duration may allow them to breed later in summer, following the molt.

The extent of preformative molt in 4 species, Rivoli's Hummingbird, Blue-throated Mountain-gem, Broad-billed Hummingbird, and Violet-crowned Hummingbird, can at least occasionally include primaries and in White-eared Hummingbird it is complete. Variation in preformative molt extent, from partial to incomplete to complete, was also documented in Broad-billed Hummingbird on the basis of initiation of primary replacement relative to body-feather replacement. Preformative molts varying to this degree and showing similar differences in feather-replacement timing have also been documented within other bird species and genera, such as those among Scolopacidae,

Tyrannidae, Sylviidae, Ptiliognathidae, Muscicapidae, Fringillidae, Passerellidae, and Cardinalidae (Miller 1933; Pyle 1997, 2008b; Jenni and Winkler 2020), perhaps as correlated with seasonal timing of fledging along with habitat use and extent of solar exposure on an annual basis (Pyle 1998, 2008b; Elrod et al. 2011; Terrill et al. 2020; Guallar et al. 2021). White-eared Hummingbird is the smallest of the 8 species treated here (Billerman 2020), and this could also be a factor in its undergoing a complete preformative molt, as molt extent in birds generally increases with decreasing body size (Kiat and Izhaki 2016).

Results of my study also help clarify previous discrepancies on timing of complete molts in these 8 southwestern hummingbird species. For example, in Broad-billed Hummingbird, I reported (Pyle 1997) that populations in the United States underwent the first molt of primaries in November–May and definitive prebasic molts in October–April; Howell (2002) concluded that the definitive prebasic molt commenced in April–September and completed in July–January, with first molt of primaries averaging later in timing; and Williamson (2002) indicated that the definitive prebasic molt occurred in May–September and the first molt of primaries occurred in July–November of the same year. Results of my study, by contrast, indicate that some birds first replace primaries during the preformative molt in August–January while others replace them during the second prebasic molt in May–September of the following year, and that the definitive prebasic molt is confined to June–October. Based primarily on banding studies the suggestions on molt timing in Broad-billed Hummingbird reported by Powers and Wethington (2020) are more consistent with the results of this study, although substantial clarification of preformative, second prebasic, and definitive prebasic molt strategies is provided here. Similar discrepancies between results reported here and those of these previous sources are found in the other 7 species. Also contrasting with previous reports, I found suspended or arrested molts to be rare in these 8 species of hummingbirds (<0.1%). Based on these results, I provide new criteria for age determination and its timing, including those related to development of definitive appearance in first-cycle males, molt limits among wing coverts, and molt clines among the remiges (Supplemental Fig. S1–S9). I found no

evidence for an identifiable second basic plumage in male Lucifer Hummingbirds and little evidence for this in Rivoli's Hummingbird, contra Pyle (1997).

Evolution of molt strategies in hummingbirds

I found no evidence for prealternate molts in these 8 species of hummingbirds, although such evidence would be better gained from banding studies; prealternate molts may not be as expected in less migratory or resident hummingbirds (Johnson and Wolfe 2018, Carnes et al. 2021). Irrespective of this, I believe that the preformative and prebasic molt strategies documented here support the interpretation of Sieburth and Pyle (2018) that the second prebasic molt has been temporally advanced in northern hummingbirds of the United States, as opposed to traditional interpretations that the first complete molt of North American hummingbirds is invariably the preformative molt. Rivoli's Hummingbird, Blue-throated Mountain-gem, and some Broad-billed Hummingbirds undergo a partial preformative molt and a complete second prebasic molt averaging earlier in timing than definitive prebasic molts, at about a year of age, a molt strategy that is common among many other birds. Likewise, complete preformative and prebasic molts during the same temporal period in White-eared Hummingbird is also consistent with the strategies of other birds. The complete second prebasic molt in this species peaks in August (Fig. 2), whereas this molt is here interpreted as peaking progressively earlier in Broad-billed Hummingbird (June), Violet-crowned Hummingbird (May), Berylline Hummingbird (March), Buff-bellied Hummingbird (February), and Lucifer Hummingbird (January), in the last species similar to the timing for the first primary molt in the 8 northern species.

Like the northern species (Sieburth and Pyle 2018), Lucifer Hummingbird is highly migratory and undergoes a partial preformative molt of feathers (e.g., those of the gorget in males) that get replaced again during the first molt of primaries in winter and early spring; the initial molt of feathers has been interpreted as a second, auxiliary preformative (formerly termed presupplemental) molt (Pyle 1997). However, in order to preserve homology under the traditional interpretation, the partial-to-incomplete molt of first cycle

Rivoli's Hummingbirds, Blue-throated Mountain-gems, and Violet-crowned Hummingbirds, and the partial-to-complete molt of first-cycle Broad-billed Hummingbirds, would also be considered auxiliary preformative molts, which would be novel interpretations for these molts. Rather, I conclude it more likely that the partial-to-complete first-cycle molts are preformative, having evolved from similar molts in ancestral Apodidae including swifts, and that the complete second prebasic molt has evolved along hummingbird lineages to become variably advanced in timing, perhaps in response to the shorter life span of hummingbirds relative to other birds (Sieburth and Pyle 2018); such interpretations have also been concluded for tropical species of hummingbirds (Pyle et al. 2015, Johnson and Wolfe 2018, Carnes et al. 2021). Further evaluation of this hypothesis can occur once molt strategies in more clades and species of hummingbirds are determined and compared with hummingbird phylogenies (e.g., McGuire et al. 2014, Stiles et al. 2017). Given the plastic nature of molt strategies found by these and other studies on avian molt to date, within genera and even within species (Johnson 1985, Voelker and Rohwer 1998, Rohwer and Irving 2011, Rohwer et al. 2011), I predict that variation in the extent and timing of preformative molts and the timing of prebasic molts in hummingbirds will be shaped more by environmental than by phylogenetic factors.

Analysis of digital images to study bird molt

As shown by the results of this study, the Macaulay Library and eBird checklists clearly provide an important resource for the investigation of avian molts and plumages, particularly with respect to sequence of remigial replacement, extent of partial and incomplete molts, timing of complete molts, and plumage-related criteria for age determination. Certain aspects of molt strategies will still need to be assessed through specimens in which, for example, age and reproductive status can be confirmed with extent of bill corrugations and information about gonads and other conditions recorded on specimen labels. Data from banding studies, furthermore, can add information on known individuals through recaptures. Analyses of individual feathers for stable isotopes and connectivity between summer and

winter grounds can also be undertaken with specimens and captured birds but not with images. Additional drawbacks to scoring molt from images include the quality of some images, making it difficult or impossible to determine precise remigial numbering, the inability to assess both wings in many cases to confirm symmetrical molt, the difficulty in assessing low levels of body-feather molt, and in the case of hummingbirds, the effects that lighting can have on iridescent display feathers as presented in single-plane images. I predict that exceptions to some of the information presented here will be found during studies using these other techniques. However, these concerns are mitigated by the substantial sample sizes of available images, resulting in adequate data despite the usability of only small proportions of these samples, and, in many cases, the ability to assess multiple images of the same individual in one or more eBird checklists.

Both specimen examination and banding studies take time and effort, as opposed to examination of online images, during which large samples can be gathered and analyzed in a short amount of time and with little expense, data are collected without having to be concerned about damaging specimens or the health of a captive bird, and voucher photographs are automatically part of the methodology and can be preserved for later examination or studies on repeatability of results. As part of this effort I undertook a validation study and found that banders and field ornithologists of varying experience levels can collect accurate data from images (Supplemental Materials file).

I encourage additional research on avian molt through examination of digital images. Here I provide a road map for such studies and I emphasize that many other questions on molt can be investigated using the Macaulay Library collection. For example, how might timing of molt in these 8 species of hummingbirds vary with respect to breeding and wintering locations or in subtropical and tropical breeding subspecies or populations (cf. Wagner 1957, Guallar and Gallés 2017, Carnes et al. 2021)? How much molt-breeding overlap may occur for birds photographed repeatedly at known nesting sites (e.g., ML174305101)? How might replacement sequence of remiges vary and be applied to the evolution of molt sequences in little-known bird families? Data from the Macaulay Library image

collection can also supplement other data sets to help answer questions related to molt intensity and duration (Rohwer et al. 2009) and to the evolution of preformative molts and formative plumages through phylogenetic comparative or ancestral state reconstruction analysis (cf. Kiat et al. 2019a), as have recently been performed based on specimens in other New World bird families such as Cardinalidae (Guallar et al. 2021) and Parulidae (Terrill et al. 2020). Finally, to best facilitate such research, I encourage those contributing images to eBird to include birds in molt or in worn plumages, even if they may not be as appealing as, for example, adult males in definitive plumage, of which >50% of hummingbird images I examined for this study referred.

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