



PREFORMATIVE MOLT EXTENT AND AGING AND SEXING CRITERIA FOR EIGHT HUMMINGBIRD SPECIES IN SOUTHEASTERN PERU

Blaine H. Carnes*, Mariamercedes Antezana Aponte¹, Renato Huayanca Munarriz¹, Ari E. Martínez^{2,3}

¹ Centro de Ornitología y Biodiversidad (CORBIDI), Santa Rita No 105, Dpto. 202, Urb. Huertos de San Antonio, Surco, Lima, Perú.

² University of California, Berkeley

³ California State University, Long Beach

E-mail: Blaine H. Carnes · blainehcarnes@gmail.com

Abstract · Little attention has been paid to molt and age criteria in hummingbirds despite their importance to numerous behavioral and ecological questions. We documented molt extent, age-specific molt patterns, plumages, percent of the bill with corrugations, the presence or absence of delayed plumage maturation, and bill color changes in males of sexually dichromatic species in eight species of lowland Amazonian hummingbirds. Molt strategies and rates of bill smoothing were similar to those of better-studied North American species, with all species showing partial preformative molts (replacing only body feathers and some wing coverts, and retaining all remiges and rectrices), and bill corrugations reducing to less than 10% of bill length in all species by the time they achieved definitive cycle basic plumage. Several species showed evidence of delayed maturation in males in regard to plumage characteristics or bill coloration.

Resumen · **Patrones de muda preformativa y criterios para determinar edad y sexo en ocho especies de colibríes en el sudeste de Perú**

Es poca la atención que se ha prestado a los criterios de muda y edad en los colibríes, a pesar de su relevancia para numerosas cuestiones de su comportamiento y ecología. Documentamos la extensión de la muda, patrones de muda específicos por edad, plumajes, porcentaje del pico con corrugaciones, presencia o ausencia de retraso en la maduración del plumaje y cambios en el color del pico en machos de ocho especies de colibríes sexualmente dicromáticas de las tierras bajas amazónicas. Las estrategias de muda y las tasas de pérdida de corrugación documentadas fueron similares a las de las especies más estudiadas de Norteamérica. Todas las especies mostraron una muda preformativa parcial, en la que solo se renuevan plumas del cuerpo y algunas coberteras alares. Las corrugaciones se redujeron a menos del 10% de la longitud del pico en todas las especies en el momento en que adquirieron el plumaje básico definitivo. Los machos de varias especies mostraron evidencia de maduración retrasada con respecto a las características del plumaje o la coloración del pico.

Key words: Bill corrugation · Formative plumage · Life history · Molt strategies · Sexual dimorphism · Taxonomy

INTRODUCTION

The description, documentation, and knowledge of molt cycles and age-related plumage differences is essential for understanding a vast variety of ornithological topics, including behavior (Doucet et al. 2007), migration ecology (Jahn et al. 2010), survivorship (Tarwater et al. 2011), and population trends (Albert et al. 2016). In temperate regions, knowledge of molt strategies has been a useful prerequisite in the development of accurate and consistent criteria for estimating the age and sex of most species (Pyle 1997a, 1997b, Jenni & Winkler 2020). Recent interest in the topic has resulted in molt and plumage descriptions of several hundred species of Neotropical landbirds (Pyle et al. 2004, Guallar et al. 2009, Wolfe et al. 2009a, 2009b, Hernández 2012, Guallar et al. 2016, Pyle et al. 2015, Johnson & Wolfe 2017, Tórrez & Arendt 2017). However, this is only a fraction of the more than 4,000 Neotropical bird species, and is biased toward understory passerines and other species that routinely fall into mist-nets (Johnson and Wolfe 2017, Rueda-Hernández et al. 2018). Molt descriptions for many other widespread genera and families remain woefully undescribed.

The family Trochilidae presents a variety of molt strategies. Many basal and some large-bodied species are reported to undergo a partial preformative molt (Zimmer 1950a, 1950b, Hu et al. 2000, Pyle et al. 2015, Johnson & Wolfe 2017), yet numerous others are reported to undergo complete preformative molts (Pyle 1997 a, Pyle et al. 2015, Johnson & Wolfe 2017). However, molts are poorly understood in many species, with often conflicting information in the literature. For example, different authors have postulated that the preformative molt extent of the genus *Phaethornis* ranges from absent (Stiles & Wolf 1974, Schuchmann 1999) to partial (Johnson and Wolfe 2017) or complete (Wolfe et al. 2009b). Even in well-known North American species, such as the Ruby-throated Hummingbird (*Archilochus colubris*) and the Rufous Hummingbird (*Selasphorus rufus*), re-

Submitted 27 November 2020 · First decision 29 January 2021 · Acceptance 10 August 2021 · Online publication 20 September 2021

Communicated by Santi Guallar & Carlos Bosque © Neotropical Ornithological Society

Table 1. WRP age cycle codes used in this study and descriptions of the time periods shown by these codes.

Cycle code	Unabbreviated	Description
FCJ	First cycle juvenile	Juvenile plumage; period before the preformative molt.
FPF	First cycle preformative molt	Preformative molt; molting from juvenile into formative plumage.
FCF	First cycle formative	Formative plumage; after the preformative molt.
SPB	Second prebasic molt	Molting from formative into second basic plumage.
DCB	Definitive cycle basic	Definitive plumage; includes second basic plumage and all subsequent basic plumages.

Table 2. Molt, plumage, bill coloration, and aging and sexing criteria for eight species of Amazonian hummingbirds. Preformative molt extent partial, and prebasic molt extent complete in all eight species. Information on presence/absence and degree of sexual dichromatism from Birds of the World accounts (Billerman et al. 2020) and Schulenberg et al. (2007). Abbreviations as in Table 1.

Species	N (recaptures)	Molt limits in FCF	Bill corrugations after FCF (maximum %)	Sexual dichromatism (presence/absence or degree)	Delayed plumage/bill color maturation in males?
White-necked Jacobin	3	Between primary and greater coverts	0% (N = 2)	Significant, but a minority of DCB females show male-like plumage	N/A
Rufous-breasted Hermit	30 (3)	Within greater coverts or between primary and greater coverts	5% (N = 12)	Minor. DCB male with dark face and throat, females with pale supercilium and malar	Yes. FCF males show less extensive dark feathering in face and throat.
Pale-tailed Barbthroat	15 (4)	Between primary and greater coverts	0% (N = 3)	Minor. DCB male with larger white patches in rectrices	Yes. Differently patterned juvenile rectrices retained until SPB.
-White-bearded Hermit	48 (10)	Within greater coverts or between primary and greater coverts	0% (N = 10)	None.	No
Great-billed Hermit	20 (5)	Within greater coverts or between primary and greater coverts	0% (N = 1)	Minimal. Males with reduced or lacking gular stripe.	No
Gray-breasted Sabrewing	13 (1)	Within greater coverts or between primary and greater coverts	0% (N = 4)	Minor. Rachides of outer three primaries thickened and flattened in DCB males	Yes. Unmodified juvenile remiges retained until SPB.
Fork-tailed Woodnymph	9	Between primary and greater coverts	0% (N = 4)	Complete dichromatism. Males iridescent on most of body, females green and gray	Yes. FCF males show incomplete iridescence in throat.
White-chinned Sapphire	1	N/A	N/A	Significant. Male with iridescent blue head and throat, red bill with dark tip	Yes. FCF males show incomplete iridescence on head and dark upper mandible.

cent studies have discovered previously unknown prealternate molt episodes (Dittmann & Cardiff 2009, Sieburth & Pyle 2018), and analyses of molt in migratory North American species and species of southwestern United States showed regular partial preformative molts (Sieburth & Pyle 2018, Pyle 2021). A number of migratory species undergo an absent-to-limited definitive prealternate molt (Dittmann & Cardiff 2009, Sieburth & Pyle 2018), but there is no evidence in the literature for prealternate molts in tropical species. The gaps in knowledge of molt strategies in hummingbirds has resulted in a paucity of studies considering age-based differences in the family

In addition to the use of molt patterns, hummingbirds can be aged by examining the bill for corrugations (Ortiz-Crespo 1972, Baltosser 1987, Yanega et al. 1997). These corrugations run the length of the bill in newly-fledged juveniles and, as the bird ages, are lost proximally from tip to base through hardening and wear, generally by at least 50% within nine months (Ortiz-Crespo 1972). In North American species, individuals greater than one year of age show corrugations on a maximum of 10% of the length of the bill (Pyle 1997, Yanega et al. 1997). Few studies have examined age-based bill corrugation measurements in Neotropical species. Johnson and Wolfe (2017) suggest that corrugations on 30% of the bill are a reasonable cutoff for showing that a bird is less than 9 months old, while Pyle et al. (2015) found that Giant Hummingbird (*Patagona gigas*) and Green-backed Firecrown (*Sephanoides sephanoides*) in Chile showed a maximum of 15 and 10% corrugations, respectively, at over one year of age. Stiles and Wolf (1974) found that corrugations in the Long-billed Hermit (*Phaethornis longirostris*) were reduced to 0% by 6 months of age.

Sexual dichromatism is found in more than 60% of hummingbird species (Billerman et al. 2020), yet in many species

the age at which males attain their definitive basic plumage is unknown, and males in some species may exhibit delayed plumage maturation, particularly if species with sex-specific characteristics in the remiges and rectrices were to undergo preformative molts that are not complete. For example, the Pale-tailed Barbthroat (*Threnetes leucurus*) exhibits sexual dichromatism in the basic rectrices (Schulenberg et al. 2007), with males showing broad white patches with a narrow black terminal band and females showing reduced white patches with a broad black subterminal band and narrow white tips. In the genus *Campylopterus*, males have thicker and more flattened rachides in the outermost primaries than females, which in Gray-breasted Sabrewing (*C. largipennis*) is currently the only known plumage difference between the sexes (Johnson & Wolfe 2017). Coloration of the mandible also appears to be linked with age and sex in some species of hummingbirds, with older males showing larger and brighter areas of coloration on the mandibles than younger males and females (Graves 2009, Stiles et al. 2017).

In order to expand our knowledge of aging and sexing criteria in hummingbirds, we document molt extent, age-specific molt patterns, percent of the bill with corrugations, patterns of sexual dichromatism of plumage, presence or absence of delayed plumage maturation, and related bill color changes in males of sexually dichromatic species in eight species common to lowland Amazonian forests: the White-necked Jacobin (*Florisuga mellivora*), the Rufous-breasted Hermit (*Glaucis hirsutus*), the Pale-tailed Barbthroat, the White-bearded Hermit (*Phaethornis hispidus*), the Great-billed Hermit (*Phaethornis malaris*), the Gray-breasted Sabrewing, the Fork-tailed Woodnymph (*Thalurania furcata*), and the White-chinned Sapphire (*Chlorestes cyanus*). Our assessment of plumage patterns emphasizes replacement patterns of wing feathers during

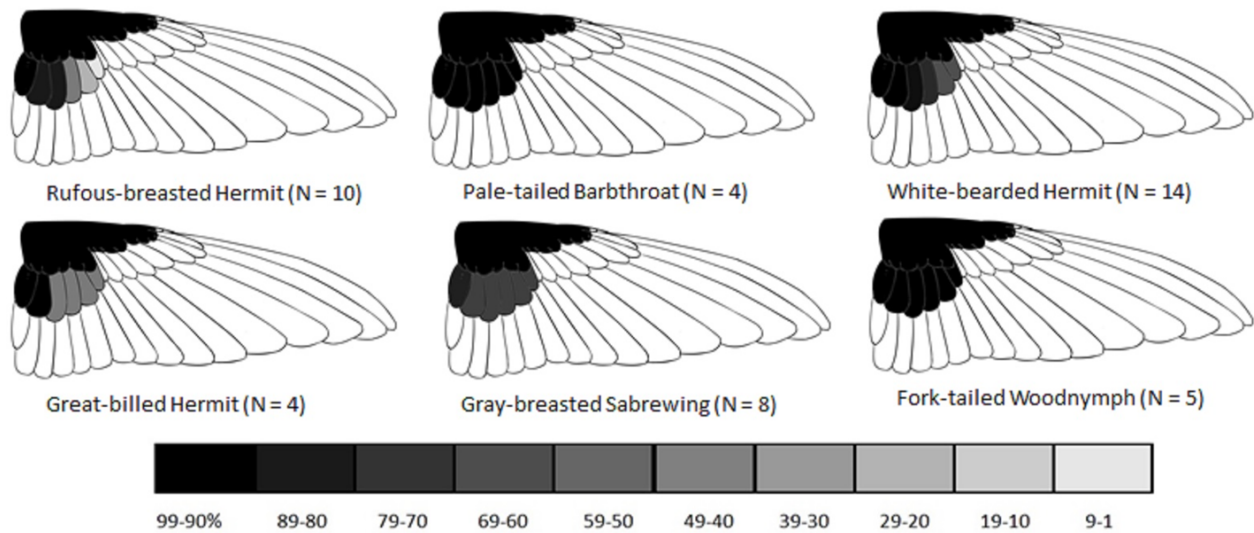


Figure 1. Frequency of feather replacement in the preformative molt of six species of Amazonian hummingbirds with a sample size of $N > 3$ FCF individuals. Gray scales represent observed replacement frequencies.

the preformative molt by focusing on differences between formative and definitive plumage, and the number of molted feathers visible in close-up digital images of the body plumage and the dorsal aspect of wings and tails.

METHODS

This study occurred as part of a larger avian community census effort at Cocha Cashu Biological Station ($11^{\circ}53'18.1''S$ $71^{\circ}24'28.6''W$) in Peru's Manu National Park from August to November 2018. Detailed description of the site and of the study plot within the site are contained in Terborgh et al. (1990). We captured hummingbirds as part of a standardized mist-netting regime with lines of 18 mist-nets (12 x 3.2 m, 36 mm mesh) along 250–350 m of trail in seven locations within a 97 ha plot, and operated the nets from dawn to dusk on three consecutive days when weather allowed, as in Terborgh et al. (1990). We also incidentally captured hummingbirds while target-netting understory mixed-species flocks by using 6 to 18 mist-nets along trails and around the roosting locations of specific flocks according to protocol in Martínez et al. (2018).

We identified captured hummingbirds using Schulenberg et al. (2007). We used the W-R-P system (Wolfe et al. 2010) as modified by Johnson et al. (2011) to categorize age classes (see Table 1 for definitions and abbreviations). We interpreted molt and plumage terminology following Humphrey and Parkes (1959) as modified by Howell et al. (2003), according to which the molt into juvenile plumage is the first prebasic (prejuvenile) molt and a second molt episode within the first annual cycle following juvenile plumage is the preformative molt (formerly defined as the first prebasic molt). The definitive molt cycle begins with the second prebasic molt and includes complete prebasic molts.

We analyzed feather replacement patterns by age/sex on all captured birds through use of photographs of the right wing, tail, and body. We photographed over 90% of captured hummingbirds; instances where individuals were released without photographs resulted from oncoming rain. We used these photographs to verify age and record the extent of the preformative molt in FCF birds, with the goal of describing

range of feathers replaced in this molt within the remiges, greater coverts, primary coverts, and rectrices. In FCF birds, we categorized replaced feathers as formative based primarily on the degree of feather wear, shape, and color/pattern. For species with a sample size > 5 photographed FCF individuals, we give a mean number of greater coverts replaced.

We follow Pyle (1997a) in describing molt extents. A “limited” molt extent refers to the replacement of some but not all body feathers, and does not include wing coverts. “Partial” refers to when some to all body feathers and wing coverts are replaced, but no flight feathers apart from perhaps the central rectrices. “Incomplete” refers to the replacement of most to all body feathers and some flight feathers, including primaries, secondaries, and outer rectrices. “Complete” refers to replacement of all feathers.

For all captured individuals, we examined for the presence of actively molting feathers, and documented the presence and extent of molt limits. We examined the bill in all captured individuals and noted the presence and extent of corrugations. In hummingbirds, males do not develop a cloacal protuberance, and although only females incubate and rear young, identification of brood patches is exceedingly difficult because in both sexes the belly is normally unfeathered and glossy (Johnson & Wolfe 2017). Due to this lack of obvious physical breeding evidence in the family, we determined sex when possible by using sexually dichromatic plumage characteristics and bill coloration, as described in Schulenberg et al. (2007) and Billerman et al. (2020). Presence/absence and degree of sexual dichromatism, and of delayed plumage maturation and related bill color changes in males in our study species are summarized in Table 2.

We were unable to mark captured hummingbirds due to not having appropriate bands for the family, and, despite past use of the technique, we did not clip rectrices due to the high number of species that incorporate the tail in courtship displays. However, with recent advances in the understanding of identifying individual birds through the use of digital photography (Pyle & Sullivan 2010, Nelson & Pyle 2013), we feel that a combination of age, sex, bill corrugations, molt pattern, and morphometric measurements (e.g., natural wing chord, length of tail to the tip of the longest rectrix, bill



Figure 2. Comparison of feather characteristics among age classes in the wings of eight species of Amazonian hummingbirds. Abbreviations as in Table 1. A) Wing of FCF female White-necked Jacobin. Note that retained juvenile primary coverts are dull green and narrow in comparison to replaced formative primary coverts. B) Wing of DCB female White-necked Jacobin without molt limits. C) FCF Rufous-breasted Hermit. Retained juvenile feathers have pale buff tips. D) DCB Rufous-breasted Hermit without molt limits. E) Wing of FCF Pale-tailed Barbthroat. Retained juvenile feathers show pale tipping. F) Wing of DCB Pale-tailed Barbthroat without molt limits. G) Wing of FCF White-bearded Hermit. Retained juvenile feathers have narrow pale tips. H) Wing of DCB White-bearded Hermit without molt limits. I) Wing of FCF Great-billed Hermit. Retained juvenile feathers have narrow buff tips. J) Wing of DCB Great-billed Hermit without molt limits. K) Wing of FCF Gray-breasted Sabrewing. Retained juvenile feathers are dull rather than iridescent green. L) Wing of DCB male Gray-breasted Sabrewing with thickened and flattened rachides to the outer primaries. M) Wing of SPB Fork-tailed Woodnymph with relatively dull retained juvenile primary coverts and iridescent formative secondary coverts. N) Wing of DCB male Fork-tailed Woodnymph without molt limits.

length from nares to tip) following Pyle (1997a), allowed us to identify all captured individuals and to account for recaptures.

RESULTS

All species showed partial preformative molts and complete definitive prebasic molts (Table 2, Figures 1–3). We found neither limited nor incomplete molts. In Figure 1 we present the frequency of feather replacement in the preformative molt in six species with a $N > 3$ photographed FCF individuals.

Bill corrugations were reduced to less than 10% of bill length after FCF in all species (Table 2, Figure 4). In most sexually dichromatic species, males did not attain full male-like characteristics until they reached DCB. One species showed evidence of changes in bill coloration with age in males (Table 2, Figure 5). We identified 16.55% of total captures as recaptures by using a combination of age, sex, bill corrugations, molt pattern, wing chord, tail length, and bill length data.

White-necked Jacobin $N = 3$ (one first-cycle): The preformative molt included all upperwing secondary coverts (Figure 2)



Figure 3. Comparison of feather characteristics among age classes in rectrix shape and pattern in three species of Amazonian hummingbirds. Abbreviations as in Table 1. A) FCF female White-necked Jacobin. FCF rectrices slightly narrower and more rounded in shape than DCB rectrices; white tip on r5 smaller with less distinct border to the blue subterminal band; pale area on outer web of r5 smaller and less distinct, and blue areas narrower, less dark, and relatively indistinct. B) DCB female White-necked Jacobin. C) FCF Rufous-breasted Hermit. FCF rectrices narrower and more pointed in shape than DCB rectrices, white tips and black subterminal band larger, and shape of the proximal end of the black subterminal band angular rather than rounded. D) DCB male Rufous-breasted Hermit. E) FCF Pale-tailed Barbthroat. FCF rectrices considerably narrower and more pointed than DCB rectrices, with larger and more indistinct areas of black coloration, and a brownish base. F) DCB male Pale-tailed Barbthroat.

All captures were females of the “speckle-throated” color morph, and the pattern and shape of juvenile rectrices differed from basic feathers, with juvenile feathers showing a narrower overall shape, a reduced subterminal blue band on r5, and reduced white in the inner web of r5 (Figure 3).

Rufous-breasted Hermit N = 27 (15 first-cycle): The preformative molt included all upperwing lesser and median coverts, and one to six greater coverts (mean = 3.7; Figures 1–2). Juvenile feathers had pale or buff tips, making molt limits easily discernible. Juvenile rectrices were narrower in shape than basic rectrices, with broader black subterminal bands and larger white tips (Figure 3). The facial pattern also seemed less developed in FCF individuals, making sex determination difficult at this age (Figure 6). Eleven of twelve DCB individu-

als showed no bill corrugations, with the remaining individual showing corrugations on 5% of the bill length. Nine of ten FCF individuals showed no bill corrugations, with the remaining individual showing corrugations on 5% of the bill length. Two FCF individuals showed corrugations running 40 and 45% of the bill length. (Figure 4).

Pale-tailed Barbthroat N = 11 (eight first-cycle): The preformative molt included all upperwing lesser, median, and greater coverts (Figures 1–2). The retained juvenile secondaries had obvious pale tips. Of note, juvenile rectrices, which are retained through the preformative molt, were differently patterned and pointed in shape in comparison to the truncate basic rectrices (Figure 3). None of the DCB and FCF individuals showed any remaining bill corrugations (Figure 4).

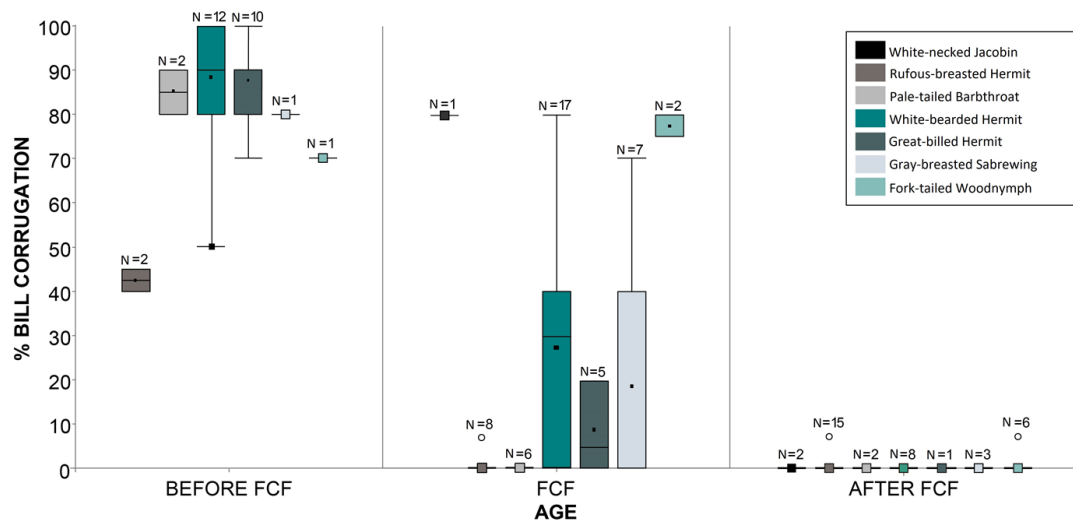


Figure 4. Box-and-whisker plots of percent of bill with corrugations in age classes before FCF, during FCF, and after FCF in seven species of lowland Amazonian hummingbirds with sample sizes $N > 1$. Abbreviations as in Table 1.



Figure 5. Body, tail, and wing of White-chinned Sapphire FPF male. Note active molt and replaced feathers confined to the iridescent feathers of the head and throat, with no synchronous remex replacement. Upper mandible was black, unlike DCB males. Abbreviations as in Table 1.

White-bearded Hermit $N = 38$ (28 first-cycle): The preformative molt included all upperwing lesser and median coverts, and two to six replaced greater coverts (mean = 5.2; Figures 1–2). Retained juvenile feathers had pale or buff tips. All DCB individuals, a SPB individual, and six of 18 FCF individuals did not show any remaining bill corrugations (Figure 4).

Great-billed Hermit $N = 15$ (14 first-cycle): The preformative molt included all upperwing lesser and median coverts, and two to six greater coverts (mean = 4.0; Figures 1–2). Retained juvenile secondaries had pale or buff tips. The one captured DCB individual and two of six FCF individuals did not show any remaining bill corrugations (Figure 4).

Gray-breasted Sabrewing $N = 12$ (eight first-cycle): The preformative molt included all upperwing lesser and median coverts, and zero to all six greater coverts (mean = 4.6; Figures 1–2). DCB individuals and four of seven FCF individuals did not show any remaining bill corrugations (Figure 4). We

measured the width of the p10 rachis in three DCB males and three FCF individuals of unknown sex. In all three DCB males, rachis width was 3.2 mm, while FCF rachis width ranged 1.5–1.7 mm (mean = 1.6 mm).

Fork-tailed Woodnymph $N = 9$ (five first-cycle): The preformative molt included all upperwing secondary coverts (Figures 1–2). FCF males had duller coloration and incomplete iridescence compared to DCB males, with patches of gray feathering on the throat (Figure 7). No DCB individuals showed bill corrugations; a SPB individual showed corrugations on 5% of the bill; and two FCF individuals showed 75% and 80% of the bill with corrugations, respectively (Figure 4).

White-chinned Sapphire $N = 1$ (first-cycle): The individual captured was a FPF male (Figure 5). Active molt was entirely within feathers of the head and throat, with no concurrent remex or rectrix molt. Replaced and actively molting formative feathers in the head and throat were blue and irides-



Figure 6. Facial pattern by age and sex in Rufous-breasted Hermit. Abbreviations as in Table 1. A) FCJ individual. B) FCF individual with maximum supercilium and malar stripe. C) FCF individual with minimum supercilium and malar stripe. D) DCB female. E) DCB male.

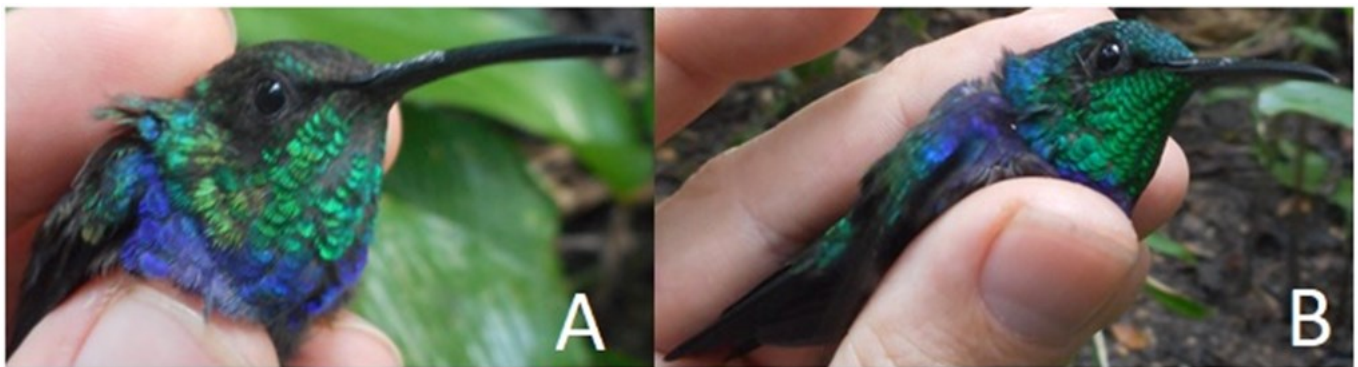


Figure 7. Age-based differences in body plumage of male Fork-tailed Woodnymphs. A) Body of FCF male with incomplete gorget. B) Body of DCB male with complete gorget.

cent, but in a patchy and incomplete pattern (Figure 5). The rectrices were entirely blue in color, as in DCB males. The bill had 80% corrugations, and the upper mandible was dark, rather than red as in DCB males.

DISCUSSION

We aged eight Amazonian hummingbird species by molt patterns and bill corrugations combined, as in other hummingbirds of tropical and temperate regions (Pyle 1997a, Pyle et al. 2015, Johnson & Wolfe 2017). Consistent with relatively well-studied temperate species of North America (Pyle 1997a, Pyle 2021) and other Amazonian lowland species of Brazil (Johnson & Wolfe 2017), the partial extent of the preformative molt in these species allowed for age assessment with molt limits.

Recent taxonomic revision and discussion of hummingbirds (McGuire et al. 2014, Stiles et al. 2017) place our study species into the Topaz clade (White-necked Jacobin), the Hermit clade (Rufous-breasted Hermit, Pale-tailed Barbthroat, White-bearded Hermit, and Great-billed Hermit), and the Emerald clade (Gray-breasted Sabrewing, Fork-tailed Woodnymph, and White-chinned Sapphire). Within the Apodiformes, a Complex Basic Strategy with partial preformative and complete definitive prebasic molts appears to be the ancestral state (Sieburth & Pyle 2018), and, as in other studies (Zimmer 1950a, Zimmer 1950b, Stiles 1980, Hu et al. 2000, Johnson & Wolfe 2017), we found partial preformative molts in species from the more basal Topaz and Hermit

clades. However, similar to other diverse Neotropical families such as *Thamnophilidae*, *Cardinalidae*, and *Thraupidae*, (Johnson & Wolfe 2017, Guallar et al. 2021), it would appear that there has been a significant amount of adaptive radiation in regard to molt in the *Trochilidae*, with inserted molts increasing and decreasing in extent according to life history strategies.

The Emerald clade, as defined by Stiles et al. (2017), shows particularly varied molt strategies, as Pyle (2021) found different strategies in three of the four major groups within the clade, with the Broad-billed Hummingbird (*Cyanthus latirostris*) in Group A, in which individuals undergo either a partial or complete preformative molt followed by a complete second prebasic molt at about a year of age, the White-eared Hummingbird (*Basilenna leucotis*) in Group B, which undergoes a complete preformative molt, and three species in Group D (Violet-crowned Hummingbird *Leucolia violiceps*, Berylline Hummingbird *Saucerottia beryllina*, and Buff-bellied Hummingbird *Amazilia yucatanensis*) that undergo protracted and partial preformative molts followed by a complete second prebasic molt that occurs at 7–10 months of age. Our study species represented three groups within the Emerald clade: Group B (Gray-breasted Sabrewing), Group C (Fork-tailed Woodnymph), and Group D (White-chinned Sapphire). Zimmer (1950c) appeared to describe White-chinned Sapphire individuals in a similar plumage stage as our captured individual, and concluded that this plumage was a stage of arrested development in males and advanced females (i.e., equivalent to the typical FCF plumage in males). Group B includes both the Gray-breasted Sabrewing

ing, which shows a partial preformative molt, and the White-eared Hummingbird, a much smaller species with a complete preformative molt in one population (Pyle 2021) and evidence of a partial preformative molt in another population (Guallar & Gallés 2017). This indicates that the differing life histories and environments experienced by these closely-related species may have a stronger effect on their molt strategies than phylogeny, similar to the proposed link between colonization of open habitats and increased molt extent in the Cardinalidae (Guallar et al. 2021).

All eight study species showed reduced or no bill corrugations after the age of FCF, similar to temperate North American species and tropical species for which these data are known (Stiles & Wolf 1974, Yanega et al. 1997, Pyle & Howell 2000). While our sample size was small for some species, we believe these results are still useful for field ornithologists. The 30% cutoff used by Johnson & Wolfe (2017) for Amazonian hummingbirds may be overly conservative, as the Giant Hummingbird is the only hummingbird currently known to show more than 10% corrugations after FCF (Pyle et al. 2015), which may result from that species' much larger body and bill than most other hummingbirds. Other large-bodied and large-billed hummingbirds (e.g., Sword-billed Hummingbird *Ensifera ensifera*) should also be examined for bill smoothing rates.

Some species with sexually dimorphic plumage may show delayed plumage maturation in males. The Pale-tailed Barbthroat and Rufous-breasted Hermit both retained juvenile rectrices in the preformative molt, which differ in pattern and shape from basic rectrices. Unlike other members of the hermit clade, males in these two species display singly, rather than at a lek (Snow 1973, Ferreira et al. 2006). Display in the Pale-tailed Barbthroat involves fanning of the tail, and at display sites DCB males displace FCF males (Snow 1973). The tail pattern in DCB males in these species may serve as an honest signal of male fitness in addition to the courtship display, as in other species of birds with complex social and signaling systems (Fitzpatrick 1998, Doucet et al. 2007). Caution is warranted with the rectrix pattern in the Rufous-breasted Hermit; however, as this species showed sexual dichromatism in the feathering of the head and face, it may show it in the tail as well. Similarly, in multiple species of *Campylopterus* and the closely related genus *Pampa*, DCB males show significantly flattened and thickened rachides among the outer primaries, and most of these species participate in lekking behavior that may include sounds produced by these modified feathers (Winker et al. 1992, Hayes 2002, Stiles et al. 2017). The difference in shape between retained juvenile primaries and definitive basic primaries could potentially lead to differences in display quality, and therefore reduce mating success in FCF males.

Additionally, Fork-tailed Woodnymph and White-chinned Sapphire males showed reduced iridescence in FCF, and the White-chinned Sapphire also showed evidence for age-based changes in mandible color. Numerous hummingbird species with areas of iridescent plumage routinely use these areas in territory defense and aggressive signaling (Ewald & Rohwer 1980, Hurley et al. 2001), but iridescent plumage may be energetically costly to grow, especially in younger individuals that are more likely to be nutritionally deficient (Meadows et al. 2012), and FCF males may signal status through extent of iridescent plumage. Age-based changes in bill coloration

could play a similar role to delayed plumage maturation. The dull coloration of the upper mandible in FCF White-chinned Sapphire males was similar to other species in the Emerald clade, in which older males exhibit larger and brighter areas of coloration on the mandibles than younger males and females (Graves 2009, Stiles et al. 2017).

Detailed determination of the timing of molt and bill smoothing in relation to the timing of breeding is made difficult by the limited available information on precise breeding periods for our study species, and the relatively brief timeframe of our study means we cannot preclude the existence of prealternate molts. Yet, we feel our results are still useful for field ornithologists. Future research on Amazonian hummingbirds is needed to gather complete information for the full annual cycle, especially regarding the timing of breeding and molt. Mark-recapture programs using appropriate-sized bands could further elucidate the progression of plumages on an individual basis, answer questions on delayed plumage maturation, and show if some older females develop male-like plumage characteristics as in other strongly sexually dichromatic families (e.g., Pipridae; Doucet et al. 2007). We encourage ornithologists working with hummingbirds to collect data on molt and plumage patterns, and bill corrugations and coloration, as these data can then serve to further refine more advanced questions of ecology, movement, and behavior. We further recommend that avian mark-recapture studies take standardized photographs of the wing, tail, and body of birds in hand. Photographs allow for detailed data to be collected at a later date and can regularly yield new insights into molt patterns and timing, even in well-studied species (Carnes & Ash 2019, Carnes et al. 2021). In addition, photographs serve as a voucher for collected data, allowing for later review of age, sex, and even species identification.

ACKNOWLEDGEMENTS

Explorer's Grant #WW-150R-17 from the National Geographic Society provided funding for this research. We thank the SERNANP for permission to work within Manu National Park. This project would not have been possible without the support of San Diego Zoo Global and the staff of Cocha Cashu Biological Station. Lauren Helton prepared the wing illustration for the figures. This paper was improved by comments from Peter Pyle, the editor, the assistant editor, and two anonymous reviewers.

REFERENCES

- Albert, SK, DF DeSante, DR Kaschube & JF Saracco (2016) MAPS (Monitoring Avian Productivity and Survivorship) data provide inferences on demographic drivers of population trends for 158 species of North American landbirds. *North American Bird Bander* 41: 133–140.
- Baltosser, WH (1987) Age, species, and sex determination of four North American Hummingbirds. *North American Bird Bander* 12: 151–166.
- Billerman, SM, BK Keeney, PG Rodewald & TS Schulenberg (2020) *Birds of the World*. Cornell Laboratory of Ornithology, Ithaca, New York, USA.
- Carnes, BH & A Ash (2019) Evidence for suspension of prebasic molt in a White-eyed Vireo. *Western Birds* 50: 52–54.
- Carnes, BH, CM Godwin, KR Foster & P Pyle (2021). Clarification of molt strategies in three *Empidonax* flycatchers. *The Wilson Jour-*

- nal of Ornithology* 133
- Dittmann, DL & SW Cardiff (2009) The alternate plumage of the Ruby-throated Hummingbird. *Birding* 41: 32–35.
- Doucet, SM, DB McDonald, MS Foster & RP Clay (2007) Plumage development and molt in Long-tailed Manakins (*Chiroxiphia linearis*): Variation according to sex and age. *The Auk* 124: 29–43.
- Ewald, PW & S Rohwer (1980) Age, coloration and dominance in non-breeding hummingbirds: A test of the asymmetry hypothesis. *Behavioral Ecology and Sociobiology* 7:273–279.
- Ferreira, ARJ, TV Smulders, K Sameshima, CV Mello & ED Jarvis (2006) Vocalizations and associated behaviors of the Sombre Hummingbird (*Aphantochroa cirrhochloris*) and the Rufous-breasted Hermit (*Glaucis hirsutus*). *The Auk* 123: 1129–1148.
- Fitzpatrick, S (1998) Birds' tails as signaling devices: Markings, shape, length, and feather quality. *The American Naturalist* 151: 157–173.
- Graves, GR (2009) Ontogeny of bill color in male streamtail hummingbirds (*Trochilus*). *Journal of Caribbean Ornithology* 22: 44–47.
- Guallar, S & A Gallés (2017) Age determination of Amethyst-throated Hummingbird (*Lampornis amethystinus*) and White-eared Hummingbird (*Hylocharis leucotis*). *Ornitología Neotropical* 28: 129–133.
- Guallar, S, E Santana, S Contreras, H Verdugo & A Gallés (2009) Paseriformes del occidente de México: morfometría, datación y sexado. *Monografías del Museu de Ciències Naturals* 5.
- Guallar, SX, A Ruiz-Sánchez, R Rueda-Hernández & P Pyle (2016) Molt strategies of ten Neotropical forest passerine species. *Wilson Journal of Ornithology* 128: 543–555.
- Guallar, S, R Rueda-Hernández & P Pyle (2021) Evolution of the preformative molt in Cardinalidae correlates with transitions from forest to open habitats. *Ornithology* 138: 1–14.
- Hayes, FE (2002) Sabre rattling at the lek: Morphological variation and its significance in the White-tailed Sabrewing (*Campylopterus ensipennis*). Pp. 23-36 in Hayes, FE & SA Temple (eds.). *Studies in Trinidad and Tobago ornithology honouring Richard ffrench*. Department of Life Sciences, University of the West Indies, Occasional Papers 11, Trinidad and Tobago.
- Hernández, A (2012) Molt patterns and sex and age criteria for selected landbirds of southwest Colombia. *Ornitología Neotropical* 23: 215–223.
- Howell, SNG, C Corben, P Pyle & DI Rogers (2003) The first basic problem: a review of molt and plumage homologies. *The Condor* 105: 635–653.
- Hu, D-S, L Joseph & D Agro (2000) Distribution, variation, and taxonomy of *Topaza* hummingbirds (Aves: Trochilidae). *Ornitología Neotropical* 11: 123–142.
- Humphrey, PS & KC Parkes (1959) An approach to the study of molts and plumages. *The Auk* 76: 1–31.
- Jahn, AE, DJ Levey, JA Hostetler & AM Mamani (2010) Determinants of partial bird migration in the Amazon basin. *Journal of Animal Ecology* 79: 983–992.
- Jenni, L & R Winkler (2020) *Moult and ageing of European passerines: Second Edition*. Bloomsbury Publishing, London, UK.
- Johnson, EI & JD Wolfe (2017) *Molt in Neotropical Birds: Life History and Aging Criteria*. CRC Press, Boca Raton, Florida, USA.
- Johnson, EI, JD Wolfe, TB Ryder & P Pyle (2011) Modifications to a molt-based ageing system proposed by Wolfe et al. (2010). *Journal of Field Ornithology* 82: 422–424.
- Martínez, AE, E Parra, O Muellerklein & VT Vredenberg (2018) Fear-based niche shifts in Neotropical birds. *Ecology* 99: 1338–1346.
- McGuire, JA, CC Witt, JV Remsen, Jr., A Corl, DL Rabosky, DL Altshuler & R Dudley (2014) Molecular phylogenetics and the diversification of hummingbirds. *Current Biology* 24: 910–916.
- Meadows, MG, TE Roudybush & KJ McGraw (2012) Dietary protein level affects iridescent colorations in Anna's Hummingbirds, *Calypte anna*. *Journal of Experimental Biology* 215: 2742–2750.
- Nelson, K & P Pyle (2013) Distribution and movement patterns of individual Crested Caracaras in California. *Western Birds* 44: 45–55.
- Ortiz-Crespo, FI (1972) A new method to separate immature and adult hummingbirds. *Auk* 89: 851–857.
- Pyle, P (1997a) *Identification guide to North American birds, Part I*. Slate Creek Press, Bolinas, California, USA.
- Pyle, P (1997b) Molt limits in North American passerines. *North American Bird Bander* 22: 49–89.
- Pyle, P (2021) Examination of images from Macaulay Library to determine avian molt strategies: A case study on eight species of North American hummingbirds. *bioRxiv* <https://doi.org/10.1101/2021.02.03.429637>.
- Pyle, P & SNG Howell (2000) Revised ageing and sexing criteria for the Blue-throated Hummingbird. *North American Bird Bander* 25: 134-137.
- Pyle, P & BL Sullivan (2010) Documenting repeated occurrence of individual birds with digital images. *Western Birds* 41: 261–265.
- Pyle, P, A McAndrews, P Vélez, RL Wilkerson, RB Siegel & DF DeSante (2004) Molt patterns and age and sex determination of selected southeastern Cuban landbirds. *Journal of Field Ornithology* 75: 136–145.
- Pyle, P, A Engilis Jr. & DA Kelt (2015) Manual for ageing and sexing landbirds of Bosque Fray Jorge National Park and North-central Chile, with notes on occurrence and breeding seasonality. *Special Publication of the Occasional Papers of the Museum of Natural Science*. Louisiana State University, Baton Rouge, Louisiana, USA
- Rueda-Hernández R, S Guallar, A Ruiz-Sánchez & P Pyle (2018) The molt issue: Where do we go from now? *Ornitología Neotropical* 29: S1–S2.
- Schuchmann, KL (1999) Family Trochilidae (Hummingbirds). Pp 468-680 in del Hoyo, J, A Elliott & DA Christie (eds.), *Handbook of the birds of the world: Barn-owls to Hummingbirds*. Lynx Edicions, Barcelona, Spain.
- Schulenberg, T. S., D. F. Stotz, D. F. Lane, J. P. O'Neill & T. A. Parker III (2007) *Birds of Peru*. Princeton University Press, Princeton, NJ.
- Sieburth, D & P Pyle (2018) Evidence for a prealternate molt-migration in the Rufous Hummingbird and its implications for the evolution of molts in Apodiformes. *The Auk: Ornithological Advances* 135: 495–505.
- Snow, BK (1973) The behavior and ecology of hermit hummingbirds in the Kanaku Mountains, Guyana. *The Wilson Bulletin* 85: 163–177.
- Stiles, FG (1980) The annual cycle in a tropical wet forest hummingbird community. *Ibis* 122: 322–343.
- Stiles, FG & LI Wolf (1974) A possible circannual molt rhythm in a tropical hummingbird. *American Naturalist* 108: 341–354.
- Stiles, FG, JV Remsen Jr. & J. McGuire (2017) The generic classification of the Trochilini (Aves: Trochilidae): Reconciling taxonomy with phylogeny. *Zootaxa* 4353: 401–424.
- Tarwater, CE, RE Ricklefs, JD Maddox & JD Brawn (2011) Pre-reproductive survival in a tropical bird and its implications for avian life histories. *Ecology* 92: 1271–1281.
- Terborgh, J, SK Robinson, TA Parker III, CA Munn & N Pierpont (1990) Structure and organization of an Amazonian forest bird community. *Ecological Monographs* 60: 213–238.
- Tórrez, MA & WJ Arendt (2017) *La muda en especies de aves seleccionadas de Nicaragua*. 1st ed. UCA Publicaciones, Managua, Nicaragua.
- Winker, K, MA Ramos, JH Rappole & DW Warner (1992) A note on *Campylopterus excellens* in Southern Veracruz, with a guide to sexing captured individuals. *Journal of Field Ornithology* 63: 339–343.
- Wolfe, JD, RB Chandler & DI King (2009a) Molt patterns, age and sex criteria for selected highland Costa Rican resident landbirds. *Ornitología Neotropical* 20: 1–9.
- Wolfe, JD, P Pyle & CJ Ralph (2009b) Breeding seasons, molt patterns, and gender and age criteria for selected northeastern Costa Rican landbirds. *Wilson Journal of Ornithology* 121: 556–

- 567.
- Wolfe, JD, TB Ryder & P Pyle (2010) Using molt cycles to categorize the age of tropical birds: an integrative new system. *Journal of Field Ornithology* 81: 186–194.
- Yanega, GM, P Pyle & GR Geupel (1997) The timing and reliability of bill corrugations for aging hummingbirds. *Western Birds* 28: 13–18.
- Zimmer, JT (1950a) Studies of Peruvian Birds. No 55. The hummingbird genera *Doryfera*, *Glaucis*, *Threnetes*, and *Phaethornis*. *American Museum Novitates* 1449: 1–51.
- Zimmer, JT (1950b) Studies of Peruvian Birds. No 56. The genera *Eutoxeres*, *Campylopterus*, *Eupetomena*, and *Florisuga*. *American Museum Novitates* 1450: 1–14.
- Zimmer, JT (1950c) Studies of Peruvian Birds. No. 58. The genera *Chlorostilbon*, *Thalurania*, *Chlorestes*, and *Chrysuronia*. *American Museum Novitates* 1474: 1–31.