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Biology of Tropical Birds

Many Central American hummingbirds can be aged and sexed by molt patterns and bill corrugations

Muchos colibríes centro americanos pueden ser sexados y su edad estimada por medio de patrones en la muda y corrugaciones en el pico

Blaine H. Carnes and *Abidas Ash*[1]

ABSTRACT. We document molt extent; age-specific molt patterns, plumages, and percent of the bill with corrugations; the presence or absence of delayed plumage maturation and bill color changes in males of some species; and molt timing in the 19 resident hummingbird species of Belize. Molt strategies and rates of bill smoothing were similar to North American species, with all species showing limited to partial preformative molts, replacing only body feathers and some wing coverts and retaining all remiges and rectrices. Extent of bill corrugations reduced to ≤10% of bill length in all species by the time definitive cycle basic plumage is achieved. Males in sexually dichromatic species showed delayed maturation in plumage characteristics and/or bill coloration, and in two dichromatic species some older females showed male-like plumage. Nine species representing multiple clades showed advanced timing to the second prebasic molt, indicating that this trait may be a proximal response to individuals not breeding during the first molt cycle. Species with advanced second prebasic molts replaced fewer wing coverts during the preformative molt than species with later molt timing.

RESUMEN. Documentamos la extensión de la muda, patrones de muda específicos por edad, plumajes y proporción del pico con corrugaciones; la presencia o ausencia de la maduración retardada del plumaje y cambios en el color del pico en machos de algunas especies; y el tiempo de la muda en 19 especies residentes de Belice. Las estrategias de la muda y las tasas de alisado del pico fueron similar a especies Norte Americanas, donde todas las especies mostraron mudas preformativas parciales limitadas, remplazando solamente las plumas del cuerpo y algunas de las coberteras de las alas y reteniendo todas las rémiges y las rectrices. La extensión de las corrugaciones del pico estuvo reducida a ≤10% de la longitud del pico para el momento en el que se alcanzó el plumaje del ciclo básico definitivo. Los machos de especies sexualmente dicromáticas mostraron maduración retardada de las características del plumaje y/o de la coloración del pico, y en dos especies dicromáticas, algunas hembras de mayor edad mostraron plumajes similares al de los machos. Nueve especies representando múltiples clados mostraron un adelantamiento en la segunda muda prebásica, indicando que esta característica puede ser una respuesta proximal a que los individuos no se reproduzcan durante la muda del primer ciclo. Las especies con la segunda muda prebásica avanzada reemplazaron menos coberteras de las alas durante la muda preformativa que las especies con muda mas tardía.

Key Words: *age; bill corrugation; delayed maturation; hummingbird; molt pattern; molt timing; sexual dichromatism*

INTRODUCTION

The importance of classifying individuals to discrete age and sex categories in studies of avian ecology cannot be overstated because behavior, habitat use, and fitness can vary dramatically between sexes and different life stages (Vitz and Rodewald 2006, Cox et al. 2014, Székely et al. 2014, Pyle et al. 2020). Age determination in most birds relies on evaluation of age-based differences in molt patterns and plumages, but molt and plumage data are unknown in many species and families, especially in tropical regions (Johnson and Wolfe 2017, Rueda-Hernández et al. 2018).

Hummingbirds, for example, are an ubiquitous component of the Neotropical avifauna, and although numerous studies have focused on their foraging ecology and status as key pollinators (e.g., Temeles et al. 2000, Leimberger et al. 2022), their movements (e.g., Volpe et al. 2014), their cognitive abilities (e.g., González-Gómez et al. 2014, Gónzalez-Gómez and Araya-Salas 2019), and their breeding behaviors, especially in lekking species (e.g., González and Ornelas 2009, Martínez-García et al. 2013), the majority of these studies have paid, at best, just cursory attention to age and potential age-related differences within species. Only a few studies have evaluated molt patterns and age criteria in Neotropical species (e.g., Wolfe et al. 2009, Pyle et al. 2015, Johnson and Wolfe 2017, Carnes et al. 2021a), and molt descriptions and age criteria exist for just over 10% of species within Trochilidae.

Although early studies offer differing and sometimes contradictory interpretations of hummingbird molt strategies, recent work focusing on hummingbird molts has shown that the majority of species in the family follow the complex basic strategy (Sieburth and Pyle 2018, Carnes et al. 2021a, Pyle 2022a), with a preformative molt inserted within the first annual cycle, just as in the more basal Apodiformes such as swifts, although some migratory hummingbirds also undergo a prealternate molt (Dittmann and Cardiff 2009, Sieburth and Pyle 2018). Similarly, prior descriptions of hummingbird molt extents assumed that the majority of species underwent a complete preformative molt, with the exception of some basal species (Wolfe et al. 2009, Pyle et al. 2015, Johnson and Wolfe 2017), but new analyses indicate that complete preformative molts are the exception rather than the rule in this family, with most species showing a limited or partial extent to this molt (Sieburth and Pyle 2018, Carnes et al. 2021a,

[1]University of Belize Environmental Research Institute

Pyle 2022a). Limited and partial extents to the preformative molt allow for the identification of individuals in their first annual molt cycle from older individuals by means of recognizing molt limits, the boundaries between the juvenile and formative feather generations.

One confounding factor in the study of hummingbird molts in northern Central America is that the timing of molt in hummingbird species of this region is concentrated in the period from February to May, but some individuals are reported to replace flight feathers outside of the typical season (Dickey and van Rossem 1938, Wagner 1957). The ability to identify molt and plumage stages relies in part on an understanding of when molts occur, and although previous authors have attempted to describe North American hummingbird molts and their timing through the use of banding data and specimen collections, banding data from the Neotropics is limited and museum collections often lack specimens in active molt (Rohwer et al. 2005). However, recent advancement in the use of digital photography to study molt (Viera et al. 2017, Panter and Amar 2021), paired with the creation of large citizen science projects such as eBird (Sullivan et al. 2009) and online photo repositories such as WikiAves and the Cornell Lab of Ornithology's Macaulay Library, has resulted in an exponential increase in the number of "digital specimens" that can supplement the use of traditional specimens in molt study (Pyle 2022a).

In addition to molt patterns, a second dependable age-related characteristic in hummingbirds is the extent of corrugations along the culmen (Ortiz-Crespo 1972, Baltosser 1987, Yanega et al. 1997, Pyle 2022b). These corrugations run the length of the bill in newly fledged juveniles, and, as the bill hardens and wears, the corrugations smooth from tip to base, generally by at least 50% within nine months (Ortiz-Crespo 1972, Yanega et al. 1997). By one year of age, North American species show corrugations on a maximum of 10% of the bill (Yanega et al. 1997, Pyle 2022b). There has been relatively little study on the extent of bill corrugations in Neotropical hummingbirds, with somewhat contradictory findings, as Johnson and Wolfe (2017) suggest corrugations on 30% of the bill as a cutoff for indicating that hummingbird species in the central Amazon basin are less than nine months old, whereas Stiles and Wolf (1974) found that corrugations in Long-billed Hermit (*Phaethornis longirostris*) were reduced to 0% by 6 months of age in Costa Rica, and Pyle et al. (2015) found that Giant Hummingbird (*Patagona gigas*) and Green-backed Firecrown (*Sephanoides sephanoides*) showed maximums of 15 and 10% corrugations, respectively, at over one year of age. Carnes et al. (2021a) found that bill corrugations reduced to less than 10% of bill length by the time of the second prebasic molt in eight Amazonian species.

Over 60% of hummingbird species exhibit sexually dichromatic characteristics (Billerman et al. 2022), yet the age at which males attain definitive appearance is unknown in most species. Carnes et al. (2021a) found evidence of delayed plumage maturation in males of four Amazonian hummingbird species that showed either strong sexual dichromatism or sex-specific characteristics in the remiges and rectrices. The age at which males obtain a definitive appearance is unknown for Central American hummingbirds, but some genera show sex-specific characters in the flight feathers; for example, males in *Pampa*, *Campylopterus*, and *Phaeochroa* have thicker and more flattened rachides in the outermost primaries than females (Johnson and Wolfe 2017, Billerman et al. 2022), and other genera such as *Anthracothorax* and *Thalurania* exhibit strong sexual dichromatism (Billerman et al. 2022). Additionally, mandible coloration appears to be linked with age and sex in some hummingbird species, with older males showing larger and brighter areas of red coloration than younger males and females (Graves 2009, Stiles et al. 2017).

In order to expand knowledge of ageing and sexing criteria in hummingbirds and allow for more detailed future behavioral and ecological work, we document molt extent; age-specific molt patterns, plumages, and percent of the bill with corrugations; the presence or absence of delayed maturation in plumage and bill color of males; and molt timing in the 19 resident species of Belize, many of which range widely throughout Mexico, Central America, and northern South America (see Table 1 for species list). Our assessment includes data from banding stations and imagery from the Cornell Laboratory of Ornithology's Macaulay Library.

METHODS

We captured hummingbirds while banding under the Monitereo de Sobreviviencia Invernal (MoSI) protocol (DeSante et al. 2005), a standardized mist-netting effort for better understanding spatial-related and habitat-related variation in the overwintering physical condition and survivorship of migratory landbirds and resident Neotropical landbirds. We collected plumage and bill data from five MoSI field sites in Belize. Black Rock Lodge (17.043°N, 89.059°W, 100 meters above sea level) included riparian forest along the Macal River, Cockscomb Basin Wildlife Sanctuary (16.781°N, 88.460°W, 67 m.a.s.l.) included advanced second-growth broadleaf forest, Shipstern Nature Reserve (18.307°N, 88.188°W, 10 m.a.s.l.) included seasonally flooded coastal woodland, Freshwater Creek Forest Reserve (18.006°N, 88.359°W, 20 m.a.s.l.) included young second-growth tropical dry forest within a matrix of active and abandoned agricultural fields, and two sites at Runaway Creek Nature Reserve (17.293°N, 88.454°W, 15 m.a.s.l.; 17.300°N, 88.449°W, 15 m.a.s.l.) included, respectively, pine savanna bordering broadleaf forest on karst hills, and broadleaf forest on karst hills bordering a seasonal wetland.

For all captured individuals, we examined for the presence of actively molting feathers in the body, tail, and wings, and documented the presence and extent of molt limits and bill corrugations. We determined sex when possible by using plumage and bill characteristics as described in Fagan and Komar (2016) and Billerman et al. (2022). Known sex characteristics are summarized in Appendix 1, as well as previously undescribed sex-related plumage traits.

When weather, capture volume, and bird condition allowed, we photographed the right wing, tail, and body of captured individuals. We recommend that hummingbirds be photographed in-hand by holding the bird low over an even, relatively dark background and out of direct sunlight so as to minimize the amount of light reflecting off of and through the wing. Direct glare and reflected light can affect the appearance of the wing feathers so that higher quality basic feathers can appear loosely textured and washed out in color like juvenile feathers, and lead to assigning an incorrect plumage class to a bird. When spreading

Table 1. List of study species, subspecies found in our study area, and if they are sexually dichromatic and/or migratory.

Species	Subspecies	Sexually dichromatic?	Migratory?
White-necked Jacobin	*Florisuga mellivora mellivora*	Yes	No
Band-tailed Barbthroat	*Threnetes ruckeri ventosus*	No	No
Long-billed Hermit	*Phaethornis longirostris longirostris*	No	No
Stripe-throated Hermit	*Phaethornis striigularis saturatus*	No	No
Brown Violetear	*Colibri delphinae*	No	No
Purple-crowned Fairy	*Heliothryx barroti*	Yes	No
Green-breasted Mango	*Anthracothorax prevostii prevostii*	Yes	Yes
Black-crested Coquette	*Lophornis helenae*	Yes	No
Canivet's Emerald	*Cynanthus canivetii canivetii*	Yes	No
Wedge-tailed Sabrewing	*Pampa curvipennis pampa*	Yes	No
Violet Sabrewing	*Campylopterus hemileucurus hemileucurus*	Yes	No
Stripe-tailed Hummingbird	*Eupherusa eximia eximia*	Yes	No
Crowned Woodnymph	*Thalurania colombica townsendi*	Yes	No
Scaly-breasted Hummingbird	*Phaeochroa cuvierii roberti*	Yes	No
Azure-crowned Hummingbird	*Saucerottia cyanocephala cyanocephala*	No	No
Cinnamon Hummingbird	*Amazilia rutila corallirostris*	Yes	No
Buff-bellied Hummingbird	*Amazilia yucatanensis yucatanensis*	Yes	Yes
Rufous-tailed Hummingbird	*Amazilia tzacatl tzacatl*	Yes	No
White-bellied Emerald	*Chlorestes candida candida*	No	No

the wing to photograph it, do so with minimal obscuring of the feathers on the upperwing surface; this often can be accomplished by holding the wing open with a finger on the underside. Cameras should be set to an image size of at least 2000 x 1500 pixels with no flash, as flash produces similar glare effects as direct sunlight.

Additionally, we followed protocols from Pyle (2022a) to review images of hummingbirds from the Cornell Lab of Ornithology's Macaulay Library. Our analysis included Macaulay Library images of the appropriate subspecies in these 19 species from Mexico, Guatemala, and Belize that had been uploaded through January 2022. For seven species with small photographic sample sizes from this geographic area (e.g., Band-tailed Barbthroat [*Threnetes ruckeri ventosus*], Black-crested Coquette [*Lophornis helenae*]), we included all images of appropriate subspecies south to Costa Rica, and for a partially migratory species with a pattern of vagrancy (i.e., Green-breasted Mango [*Anthracothorax prevostii prevostii*]) we included all images from the United States. We excluded misidentified images (< 5% of the ML catalogue for each species) from our analysis and flagged these images for the eBird review process.

We only recorded data from images in which individuals could be assessed for both age and molt status, in which all remiges were visible or in active molt. We excluded images of the same individual from within the same month based on molt and plumage status, date, location, eBird checklist data, appearance, and bill pattern. Individuals that were recorded over multiple months at a single location were assessed in each month of occurrence. Because banding hummingbirds in the field was not feasible, and the photos we reviewed from the Macaulay Library did not include marked birds, we consider each photograph used in analysis as separate samples rather than separate individuals, with the exception of a few well-documented individuals.

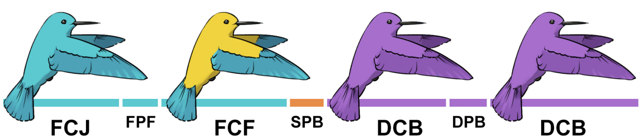
We used these photographs in combination with previously described age characteristics of hummingbirds, such as bill corrugation extent and the buff or pale tips found on juvenile feathers in many species, to both determine age characteristics by species and verify the ages of birds in our sample. As in some other studies of molt in Neotropical birds (e.g., Ruíz-Sánchez et al. 2012), determining basic plumage characteristics for separating birds in their first molt cycle from later molt cycles does not require a large initial sample size.

We categorized age classes using the WRP system (Wolfe et al. 2010) as modified by Johnson et al. (2011) and Pyle et al. (2021). To age a bird in this context means to establish a plumage class that correlates, sometimes loosely, to the actual age of an individual. The progression of hummingbird molts, their approximate extents, and the resulting plumage classes' corresponding WRP codes is shown in Fig. 1. Molt and plumage terminology follows Humphrey and Parkes (1959) as modified by Howell et al. (2003). Our descriptions of molt extent follow Pyle (2022b), in which "limited" refers to replacement of some but not all body feathers and no flight feathers, "partial" refers to replacement of some to all body feathers and wing coverts, but not flight feathers, and "complete" refers to replacement of all feathers.

After assigning age classes to the hummingbirds in our sample, we analyzed photographs of individuals in first-cycle formative plumage and individuals that had just begun the second prebasic molt but only replaced a few feathers, with the goal of describing the range of feathers replaced in the preformative molt within the remiges, greater coverts, primary coverts, and rectrices. We categorized replaced feathers as formative based primarily on sequence of replacement in the wing coverts and remiges as described by Pyle (2022), degree of feather wear, shape, and color/pattern.

We next compared the extent of bill corrugation by age class in order to determine the maximum corrugation amount by age class in each species, and examined the timing of molts in order to determine if any of these 19 hummingbird species showed differences in the timing of the second and definitive prebasic molts, as shown by some North American species. This examination of molt timing appeared to also show a pattern

Fig. 1. The progression of molts and their resulting plumages in hummingbirds. The first plumage following the prejuvenile molt is first-cycle juvenile plumage (FCJ). Not long after fledging, or perhaps while still in the nest in some species, they undergo the first-cycle preformative molt (FPF), a molt of limited to partial extent in which body feathers and some to all wing coverts are replaced but the juvenile remiges, rectrices, and primary coverts are retained, resulting in first-cycle formative plumage (FCF). The next molt in sequence, the second prebasic molt (SPB), entails the complete replacement of all feathers and results in definitive-cycle basic plumage (DCB). Subsequent molts are also complete in replacement and referred to as definitive prebasic molts (DPB) and also result in definitive-cycle basic plumage (DCB).



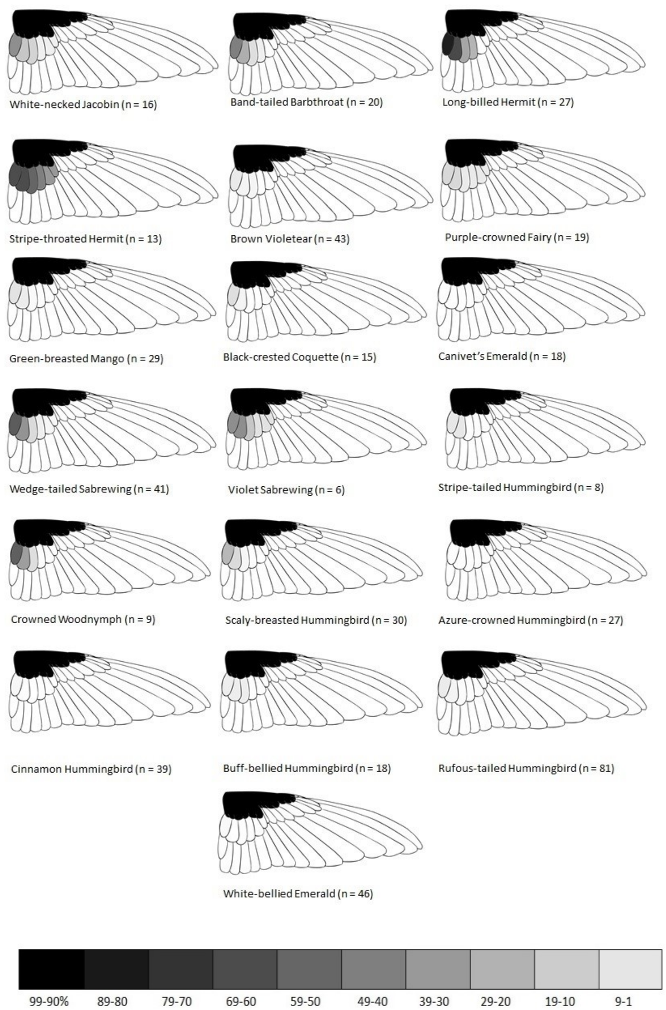
of different extents of the preformative molt between species with similar annual timing to the second and definitive prebasic molts versus those with advanced timing to the second prebasic molt. We used a generalized linear mixed effects model (Bolker et al. 2009) following a poisson distribution in r (version 4.2.3; R Core Team 2022) using the "glmer" function in the lme4 package (Bates et al. 2015) to assess the relationship between total feather replacement and molt timing. Species acted as a random effect to account for variance in feather replacement between species that is not attributable to molt timing.

RESULTS

All species showed limited to partial preformative molts, which included the replacement of at least all upperwing lesser coverts and some median coverts, and complete subsequent prebasic molts (Table S1). In Fig. 2, we present the frequency of feather replacement in the preformative molt. Bill corrugations had reduced to ≤ 10% of bill length by definitive cycle basic plumage in all 19 species (Table S1). In sexually dichromatic species, males did not attain full male-like plumage characteristics until the second prebasic molt, especially when those characteristics affected the remiges and rectrices or included large areas of iridescent plumage (Table S1). In all 5 species with sexually dichromatic coloration in the bill, males showed delayed maturation in bill color (Table S1). We describe age and sex criteria by species and provide a primer in Appendix 1. In at least two species (White-necked Jacobin [*Florisuga mellivora*] and Green-breasted Mango), some females in definitive-cycle basic plumage have a male-like plumage.

Male-like plumages are well-known in females of White-necked Jacobin (see Falk et al. 2021), but less well-documented in females of Green-breasted Mango. Our determination of male-like plumages in females of this species relied entirely upon photographs showing birds in a male-like plumage on nests because male hummingbirds do not participate in incubation and raising offspring. We acknowledge that this creates some

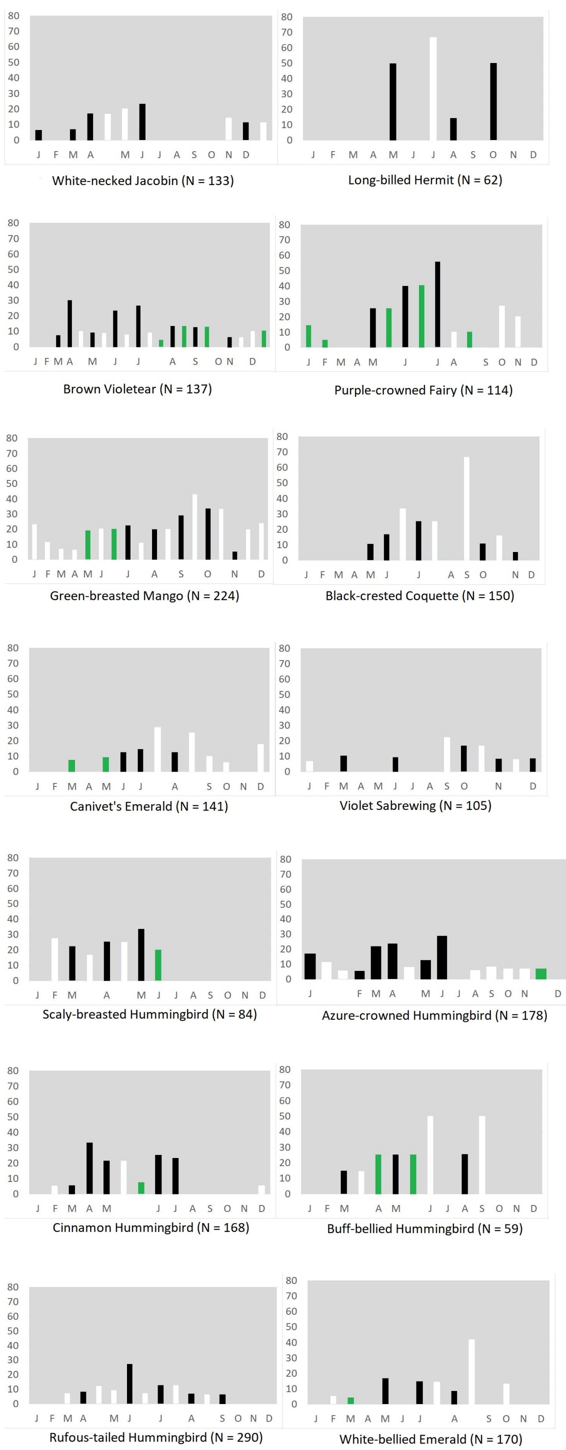
Fig. 2. Frequency of replacement in wing feathers during the preformative molt in 19 Central American hummingbird species. Gray scales represent observed replacement frequencies. See Table 1 for species scientific names.



uncertainties in regard to the determination of sex in this and other species as based solely on plumage characteristics, but believe that our results are still a useful starting point for studying the plumages of these species.

We examined a total of 15,715 images from the Macaulay Library catalogue of these 19 hummingbird species, which included images of sufficient quality to assess age category and molt status in 2242 individuals by month, and we also examined 522 in-hand photographs of 202 individuals by month from banding operations. This includes 505 total first-cycle individuals (prior to the second prebasic molt), 54 individuals undergoing preformative molt, 147 individuals undergoing the second prebasic molt, 1840 individuals in definitive basic plumage, and 137 individuals undergoing definitive prebasic molt. We were able to assess individuals from each species in at least 11 months of the year, with only White-necked Jacobin and Long-billed Hermit not represented in a month.

Fig. 3. Timing of molts in 14 Central American hummingbird species. Bars represent proportion of the entire monthly sample undergoing each molt. Black bars indicate individuals undergoing the definitive prebasic molt (DPB), white bars indicate individuals undergoing the second prebasic molt (SPB), and green bars indicate individuals undergoing the preformative molt (FPF). See Table 1 for species scientific names.



Total individuals by month were highest in the November–March period, even when accounting for individuals from banding operations.

Individuals undergoing the preformative molt all showed ≥ 20% of the bill with corrugations, and 18 of 23 individuals showed ≥ 50% corrugations. Timing of the preformative molt in most species appeared to occur soon after fledging, although in some individuals this molt may initiate while still in the nest and overlap with prejuvenile molt (Fig. 3). Timing of the definitive prebasic molt in most species appears to occur either in the same period of the year as the preformative molt, or slightly afterward (Fig. 3). Nine species showed advanced timing to the second prebasic molt, while 5 species showed similar timing to the second and definitive prebasic molts (Fig. 3). Sample sizes of molting birds were too small in the remaining 5 species to determine the respective timing of molts.

Species with similar timing to the second and definitive prebasic molts replaced more greater coverts in the preformative molt (X = 0.958 greater coverts replaced, +/- 0.153) than did species with advanced timing to the second prebasic molt (X = 0.153 greater coverts replaced, +/- 0.040). We found this relationship between total feather replacement and molt timing to be significant (est. = 1.8586, std error = 0.5413, z value = 3.433, p-value = 0.0006).

Species accounts

White-necked Jacobin (N = 133; 16 first-cycle)
The preformative molt included a limited number of body feathers and 0 to 3 inner greater coverts (mean = 1.0; Fig. 2). Juvenile characteristics retained into first-cycle formative plumage include a variable number of turquoise-blue feathers on the head and part or all of the buff malar stripe (Fig. S1). The tail pattern differs by age and sex, with definitive-cycle basic males showing mostly white rectrices with thin blue edging, definitive-cycle basic "blue-morph" females showing white rectrices with thick blue edging, and first-cycle formative birds showing thick blue edging and gray centers to the central rectrices (Fig. S1). Sexual dimorphism in this species is well-documented (see Falk et al. 2021), but the age at which females attain their definitive color morphs is unknown. Two females undergoing the second prebasic molt were transitioning from male-like formative plumage to a "speckle-throated" second basic plumage (Fig. S1). Bill corrugations reduced to 0% by the time of the second prebasic molt. The second and definitive prebasic molts have similar timing (Fig. 3).

Band-tailed Barbthroat (N = 72; 20 first-cycle)
The preformative molt included 0 to 4 inner greater coverts (mean = 1.0; Fig. 2, 4A). Retained juvenile feathers have a pale tip and are dull in color, rather than metallic bronze-green, but caution is warranted because basic inner secondaries have narrow buff edging (Fig. 4A-B, S2). Juvenile rectrices are narrow and sharply pointed in comparison to basic rectrices (Fig. 5A-B). Bill corrugations reduced to 0% by the second prebasic molt.

Long-billed Hermit (N = 62; 27 first-cycle)
The preformative molt included 1 to 6 inner greater coverts (mean = 2.24; Fig. 2, 4C). Retained juvenile feathers had pale or buff tips and were dull in color rather than a metallic green (Fig. 4C-D, S3). Juvenile rectrices are slightly narrower and looser in texture than basic rectrices (Fig. 5C-D). Bill corrugations reduced

Fig. 4. Comparison of feather characteristics among age classes in the wings of 9 Central American hummingbird species captured during MoSI banding operations. (A) First-cycle formative Band-tailed Barbthroat (*Threnetes ruckeri ventosus*); note dull coloration of retained juvenile outer greater coverts versus metallic green formative inner greater coverts. (B) Definitive-cycle basic Band-tailed Barbthroat; note lack of contrast within the wing. (C) First-cycle formative Long-billed Hermit (*Phaethornis longirostris longirostris*); note dull retained juvenile outer greater coverts with pale tip versus green formative inner greater coverts. (D) Definitive-cycle basic Long-billed Hermit; note lack of contrast in the wing. (E) First-cycle formative Purple-crowned Fairy (*Heliothryx barroti*); note retained juvenile outer greater coverts with metallic green tip and dull center, versus entirely metallic green formative inner greater coverts, and remiges with pointed shape, loose texture, and considerable wear. (F) Definitive-cycle basic Purple-crowned Fairy; note coverts entirely metallic green and remiges broad with tight texture. (G) First-cycle formative Wedge-tailed Sabrewing (*Pampa curvipennis pampa*); note dull retained juvenile outer greater coverts versus metallic green formative inner coverts, and unmodified rachides to the outer primaries. (H) Definitive-cycle basic male Wedge-tailed Sabrewing; note coverts entirely metallic green and thickened rachides to outer primaries. (I) First-cycle formative female Violet Sabrewing (*Campylopterus hemileucurus hemileucurus*); note dull coloration of primary coverts versus metallic green greater coverts. (J) First-cycle formative male Violet Sabrewing; note dull primary coverts outer greater coverts. Outer two primaries may have been accidentally replaced on this individual. (K) Definitive-cycle basic male Violet Sabrewing; note metallic green greater coverts, thickened rachides to the outer three primaries.

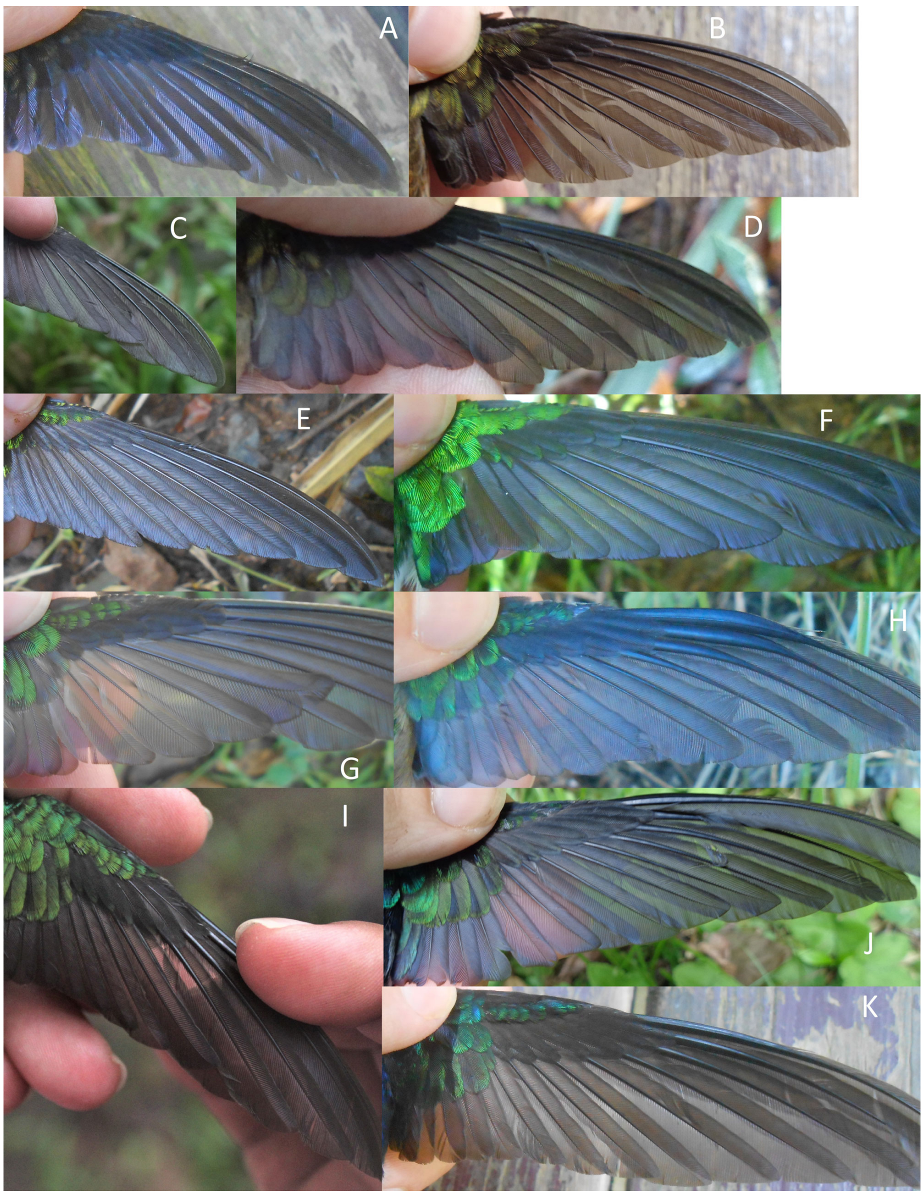


Fig. 5. Comparison of feather characteristics among age classes in rectrix shape and pattern in 9 Central American hummingbird species captured during MoSI banding operations. Abbreviations as in Table 1. (A) First-cycle formative Band-tailed Barbthroat (*Threnetes ruckeri ventosus*); note thin, pointed shape and dark pointed notch in white terminal band. (B) Definitive-cycle basic Band-tailed Barbthroat; note broader shape and blocky shape to white terminal band. (C) First-cycle formative Long-billed Hermit (*Phaethornis longirostris longirostris*); note loose texture, narrow notch to dark subterminal band, and extensive buff-brown color in uppertail coverts. (D) Definitive-cycle basic Long-billed Hermit; note broad notch to dark subterminal band and bands of buff, black, and green in uppertail coverts. (E) First-cycle formative Stripe-throated Hermit (*Phaethornis striigularis saturatus*); note sharp angle to pale subterminal band, uppertail coverts mostly brown. (F) Definitive-cycle basic Stripe-throated Hermit; note broad angle to pale subterminal band, uppertails coverts mixed green and brown. (G) First preformative molt male Purple-crowned Fairy (*Heliothryx barroti*); note shape intermediate to female and definitive-cycle basic male, and white outer rectrices. (H) First-cycle formative female Purple-crowned Fairy; note long, thin shape and black bands at base of outer rectrices. (I) Definitive-cycle basic male Purple-crowned Fairy; note short, broad shape and white outer rectrices. (J) First-cycle formative male Wedge-tailed Sabrewing (*Pampa curvipennis pampa*); note limited white on outer rectrix. (K) Definitive-cycle basic female Wedge-tailed Sabrewing; note broad pale tip and outer edge on outermost rectrix, some pale tipping on r4. (L) Definitive-cycle basic male Wedge-tailed Sabrewing; note narrow shape and pale coloration limited to edge of outermost rectrix. (M) First-cycle formative female Violet Sabrewing (*Campylopterus hemileucurus hemileucurus*); note pointed shape and concave boundary of white tip. (N) Definitive-cycle basic male Violet Sabrewing; note broad shape and broad boundary to white tip. (O) First-cycle formative Scaly-breasted Hummingbird (*Phaeochroa cuvierii roberti*); note narrow shape and concave boundary of white tip. (P) Definitive-cycle basic Scaly-breasted Hummingbird; note broad shape, notched boundary to white tip. (Q) First-cycle formative Buff-bellied Hummingbird (*Amazilia yucatanensis yucatanensis*); note loose texture, narrower shape, and diffuse dark tip. (R) Definitive-cycle basic Buff-bellied Hummingbird; note broad shape and distinct bronze-green tip. (S) First-cycle formative White-bellied Emerald (*Chlorestes candida candida*); note pointed shape, less-bright pale tips, and narrow subterminal band. (T) Definitive-cycle basic White-bellied Emerald; note broad shape, broad pale tips, and broad subterminal band.

to 0% by the second prebasic molt. The second and definitive prebasic molts have similar timing (Fig. 3).

Stripe-throated Hermit, Phaethornis striigularis (N = 68; 13 first-cycle)
The preformative molt included 0 to 6 greater coverts (mean = 3.3; Fig. 2). Retained juvenile feathers are duller in coloration than the greenish-brown formative feathers and had pale or buff tips, but caution is warranted as basic inner secondaries also have narrow pale tipping (Fig. S4). Juvenile rectrices are narrower and more pointed in shape than basic rectrices (Fig. 5E-F). With the exception of one individual with 5% corrugations, bill corrugations reduced to 0% by definitive-cycle basic plumage.

Brown Violetear, Colibri delphinae (N = 137; 43 first-cycle)
The preformative molt included 0 to 3 inner greater coverts (mean = 0.15; Fig. 2, S5). Retained juvenile wing coverts had a pale tip, especially visible on the greater coverts and sometimes in the inner secondaries (Fig. S5). Bill corrugations reduced to 0% by the second prebasic molt. The second and definitive prebasic molts have similar timing (Fig. 3).

Purple-crowned Fairy, Heliothryx barroti (N = 114; 19 first-cycle)
The preformative molt included 0 to 6 inner greater coverts (mean = 0.62; Fig. 2, 4E). Juvenile wing coverts are a comparatively dull bronze-green, rather than the metallic emerald green of basic feathers (Fig. 4E-F, S6). Rectrix shape and pattern differs by age and sex, with definitive-cycle basic males having a short, broad tail with the outer three rectrices white and the inner two black; females having a long, narrow tail with the outer three rectrices white with one black bar, and the inner two black; and first-cycle males having a tail of intermediate length with a color pattern matching that of definitive-cycle basic males (Fig. 5G-I). Bill corrugations reduced to 0% by the second prebasic molt. First-cycle formative males retain some brown juvenile feathers in the head and do not show the full male-like head pattern (Fig. S6). The definitive prebasic molt occurs May–July, while the second prebasic molt occurs between August–November (Fig. 3).

Green-breasted Mango (N = 224; 29 first-cycle)
The preformative molt included 0 to 2 inner greater coverts (mean = 0.20; Fig. 2, S7). Juvenile wing coverts are comparatively duller green than basic feathers, with less iridescence (Fig. S7). Males showed delayed plumage maturation, with iridescent body plumage not appearing until the second prebasic molt (Fig. S7). Four definitive-cycle basic females on nests showed male-like body plumage, but no individuals showed intermediate plumage (Fig. S7). Bill corrugations reduced to 0% by the second prebasic molt. The definitive prebasic molt occurs from June to November, but the second prebasic molt can occur throughout the year, likely resulting from the timing of when birds fledge and protracted individual molts (Fig. 3). One vagrant individual overwintering in the southeastern United States showed a protracted second prebasic molt with a duration ≥ 133 days.

Black-crested Coquette (N = 150; 15 first-cycle)
The preformative molt included 0 to 2 inner greater coverts (mean = 0.17; Fig. 2, S8). Juvenile feathers are comparatively duller green than basic feathers, with less iridescence (Fig. S8). Males showed delayed maturation in both plumage and bill color, with the upper mandible not becoming mostly red until during or after the second prebasic molt (Fig. S8). Bill corrugations reduced to 0% by definitive-cycle basic. The second and definitive prebasic molts occur in similar time periods, but the peaks of the molting periods are offset, with the second prebasic molt peaking later in the year (Fig. 3).

Canivet's Emerald, Cynanthus canivetii (N = 141; 18 first-cycle)
All greater coverts were retained in the preformative molt, leading to molt limits between the median and greater coverts (Fig. 2, S9). Juvenile feathers are comparatively duller green than basic feathers, with less iridescence (Fig. S9). Males showed delayed maturation in both plumage and bill color, with the body plumage showing partial and patchy iridescence and the bill not becoming fully red until after the second prebasic molt (Fig. S9). Bill corrugations reduced to 0% by definitive-cycle basic. The definitive prebasic molt occurs from June to August, while the second prebasic molt occurs from July to December, ~7 months after the preformative molt (Fig. 3).

Wedge-tailed Sabrewing, Pampa curvipennis (N = 136; 41 first-cycle)
The preformative molt included 0 to 6 inner greater coverts (mean = 1.31; Fig. 2, 4G). Juvenile wing coverts are a dull green, while formative and basic wing coverts are a metallic green (Fig. 4G-H, S10). Tail pattern differs by age and sex, with definitive-cycle basic males having long, graduated green and black rectrices with a rounded tip, females with a more-rounded tail shape and pale gray tips to the outer two rectrices, and some first-cycle males with narrow, pointed rectrices showing variable amounts of white in the outer two rectrices (Fig. 5J-L). Males showed delayed plumage maturation, with first-cycle formative individuals not showing modified rachides to the outer primaries until the replacement of the juvenile primaries during the second prebasic molt, and showing intermediate or female-like tail patterns. Bill corrugations reduced to 0% by definitive-cycle basic.

Violet Sabrewing, Campylopterus hemileucurus (N = 105; 6 first-cycle)
The preformative molt included 0 to 6 inner greater coverts (mean = 1.44; Fig. 2, 4I-J). Juvenile wing coverts are a dull green, while formative and basic wing coverts are a bright metallic green (Fig. 4I-J, S11). Tail pattern differs by age and sex: definitive-cycle basic males have broad black rectrices with large white tips on the outer three, definitive-cycle basic females have broad green to black rectrices with broad white tips, first-cycle males have broad green to black rectrices with large white tips on the outer three, and first-cycle females have narrow, pointed green to black rectrices with white tipping on the outer four (Fig. 5M-N). Males showed delayed plumage maturation, with first-cycle formative individuals showing incomplete violet iridescence and lacking modified rachides to the outer primaries (Fig. S11). Bill corrugations reduced to 0% by the second prebasic molt. The second and definitive prebasic molts show similar timing (Fig. 3).

Stripe-tailed Hummingbird, Eupherusa eximia (N = 64; 8 first-cycle)
The preformative molt included 0 to 2 inner greater coverts (mean = 0.18; Fig. 2, S12). Juvenile wing coverts are comparatively duller green than basic feathers, with less iridescence, and juvenile secondaries are a washed-out rufous in comparison to the bright rufous coloration of basic secondaries (Fig. S12). Males showed

delayed plumage maturation, with first-cycle formative individuals showing incomplete iridescence, especially in the gorget (Fig. S12). Bill corrugations reduced to 0% by the second prebasic molt.

Crowned Woodnymph, Thalurania colombica (N = 76; 9 first-cycle)
The preformative molt included 0 to 3 greater coverts (mean = 1.13; Fig. 2, S13). Juvenile wing coverts are a dull green in color, contrasting with the metallic green formative coverts of females and violet formative coverts of males (Fig. S13). Males showed delayed plumage maturation, with first-cycle formative individuals showing duller coloration and incomplete iridescence, especially within the gorget, than definitive-cycle basic individuals (Fig. S13). Bill corrugations reduced to 0% by definitive-cycle basic.

Scaly-breasted Hummingbird, Phaeochroa cuvierii (N = 84; 30 first-cycle)
The preformative molt included 0 to 3 inner greater coverts (mean = 0.45; Fig. 2, 6L). Retained juvenile wing coverts have pale tips (Fig. 6L-M, S14). Juvenile rectrices are narrow and loosely textured, with convex white tips, while basic rectrices are broad with a jagged pattern to the white tips (Fig. 5O-P). Males showed delayed plumage maturation, with first-cycle formative individuals not showing modified rachides in the outer primaries (Fig. 6L, S14). Bill corrugations reduced to 0% by definitive-cycle basic. The second and definitive prebasic molts showed similar timing (Fig. 3).

Azure-crowned Hummingbird, Saucerottia cyanocephala (N = 178; 27 first-cycle)
All greater coverts were retained in the preformative molt, leading to molt limits between the median and greater coverts (Fig. 2, S15). Juvenile feathers are comparatively duller green than basic feathers, with less iridescence (Fig. S15). Bill corrugations reduce to 0% by the second prebasic molt. The definitive prebasic molt occurs from January to June, while the second prebasic molt occurs between August and April, ~7–10 months following the preformative molt (Fig. 3).

Cinnamon Hummingbird, Amazilia rutila (N = 168; 39 first-cycle)
With the exception of one individual that replaced the innermost greater covert, all greater coverts were retained in the preformative molt, leading to molt limits between the median and greater coverts (Fig. 2, S16). Juvenile feathers are comparatively duller green than basic feathers, with less iridescence (Fig. S16). Males showed delayed maturation in bill color, with most first-cycle formative males showing mixed black and pink coloration to the upper mandible (Fig. S16). Bill corrugations reduced to 0% by the second prebasic molt. The definitive prebasic molt occurs from March to July, while the second prebasic molt occurs December–May (Fig. 3).

Buff-bellied Hummingbird, Amazilia yucatanensis (N = 59; 18 first-cycle)
The preformative molt included 0 to 3 inner greater coverts (mean = 0.2; Fig. 2, 6N). Juvenile wing coverts are comparatively dull green, rather than the bright metallic green of basic feathers (Fig. 6N-O, S17). Juvenile rectrices are narrow with dusky bronze-green tipping, and basic rectrices are broad, with well-defined bronze-green edging (Fig. 5Q-R). Males showed delayed maturation in bill color, with most first-cycle formative males showing mixed red and black coloration to the upper mandible (Fig. S17). Bill corrugations reduced to 0% by definitive-cycle basic. Most individuals underwent the definitive prebasic molt March–May, while the second prebasic molt peaked in June–September (Fig. 3).

Rufous-tailed Hummingbird, Amazilia tzacatl (N = 290; 81 first-cycle)
The preformative molt included 0 to 3 inner greater coverts (mean = 0.13; Fig. 2, 6P). Juvenile wing coverts are a dull green, rather than the metallic bronze-green of basic feathers (Fig. 6P-Q, S18). Juvenile rectrices have washed-out bronze edging, sometimes broken at the tip, while basic rectrices have comparatively broad bronze edging (Fig. S18). Males had delayed maturation in plumage and bill color, with the gorget often having a "frosted" appearance rather than the solidly iridescent green of definitive-cycle basic males, and the upper mandible regularly showing limited red coloration, rather than the extensive red of definitive-cycle basic males (Fig. S18). Bill corrugations typically reduced to 0% by definitive-cycle basic, but 2.67% of definitive-cycle basic individuals showed a maximum of 10% corrugations. The definitive prebasic molt occurred April–September, with a peak in June–July, while the second prebasic molt occurred March–Aug, with peaks in April–May and July (Fig. 3).

White-bellied Emerald, Chlorestes candida (N = 170; 46 first-cycle)
The preformative molt included 0 to 2 inner greater coverts (mean = 0.04; Fig. 2, 6R). Juvenile wing coverts are a washed-out dull green, while formative and basic wing coverts are a metallic green (Fig. 6R-S, S19). Juvenile rectrices are narrow and bronze-green with a narrow dark subterminal band and small white tip, while basic rectrices are broad and bronze in color, with a more well-defined subterminal band and larger white tip (Fig. 5S-T). Bill corrugations typically reduced to 0% by definitive-cycle basic, but 4.42% of definitive-cycle basic individuals showed a maximum of 10% corrugations. The definitive prebasic molt occurred May–August, while the second prebasic molt occurred July–February (Fig. 3).

DISCUSSION

We showed that these 19 Central American hummingbird species can be aged and sexed by molt and plumage patterns, bill coloration, and bill corrugations, much as other recent studies of hummingbirds in temperate and tropical regions have shown (Johnson and Wolfe 2017, Carnes et al. 2021a, Pyle 2022a). These hummingbird species show similarities in their molts to other species from their respective clades in Peru and North America, with differences in timing likely resulting from differences in breeding regimes as correlated with latitude, seasonality, and phenologies of flowering plants.

Early studies of hummingbird molt in the region noted multiple peaks of molting birds within the calendar year (Dickey and van Rossem 1938, Wagner 1957), but did not recognize that there could be differential timing to the second and definitive prebasic molts, as was the case for some hummingbirds studied by Pyle (2022a). There is little available information on the timing of the preformative molt in tropical hummingbirds. Many recently fledged hummingbirds appear to already be in first-cycle

Fig. 6. (L) Second prebasic molt Scaly-breasted Hummingbird (*Phaeochroa cuvierii roberti*); note pale tips to retained juvenile feathers. (M) Definitive prebasic molt Scaly-breasted Hummingbird; note entirely metallic green feathers among the coverts, modified rachides to outer primaries. (N) First-cycle formative Buff-bellied Hummingbird (*Amazilia yucatanensis yucatanensis*); note loosely-textured and dull green greater coverts. (O) Definitive-cycle basic Buff-bellied Hummingbird; note metallic green greater coverts. (P) First-cycle formative Rufous-tailed Hummingbird (*Amazilia tzacatl tzacatl*); note loosely-textured and dull green greater coverts. (Q) Definitive-cycle basic Rufous-tailed Hummingbird; note metallic green greater coverts. (R) First-cycle formative White-bellied Emerald (*Chlorestes candida candida*); note greater coverts with loose texture, limited dull green color. (S) Definitive-cycle basic White-bellied Emerald; note greater coverts with green color.

formative plumage, and the high percentage of bill corrugations on individuals undergoing the preformative molt suggests that this molt can overlap with the prejuvenile molt in some individuals, as occurs in some Parulidae species (e.g., Wilson's Warbler, *Cardellina pusilla*; Pyle 2022b). Previous observers could have mistakenly assumed that these overlapping molts in hummingbirds were a single molt episode, similar to early descriptions of the prealternate molts in some migratory flycatchers (see Carnes et al. 2021b, Pyle and Carnes 2022), leading to the misinterpretation of the second prebasic molt several months later as a complete preformative molt.

The advanced timing to the second prebasic molt shown by some species may have evolved out of a need to breed early in life. Other recent studies of hummingbird molt have found an advanced timing to the second prebasic molt in species in which males produce mechanical sounds with the remiges and/or rectrices during aggressive interactions and courtship displays (Sieburth and Pyle 2018, Pyle 2022a). The shape and structure of basic flight feathers appears essential to the production of mechanical sounds in display dives (Clark et al. 2011, 2018), indicating that males with juvenile flight feathers have little or no reproductive success. In the Bee clade, males are much smaller than females, engage in display dives and highly aggressive behavior, and have lower annual survivorship and shorter lifespans than females (Calder et al. 1983, Mulvihill et al. 1992). A potential loss of productivity in a year of what is already a reduced lifespan has likely driven the evolution of the advanced molt timing in the Bee clade. Two of our study species with advanced timing to the second prebasic molt (Black-crested Coquette and Canivet's Emerald) are from genera where males are known to engage in display flights (Stiles and Skutch 1989), and others, such as the four species from Group D of the Emerald clade, are known to be highly aggressive (Billerman et al. 2022). In contrast, males of all age classes in Long-billed Hermit, which has similar timing to the second and definitive prebasic molts, can have annual survivorship of 60% or higher (Stiles 1992), likely reducing the need for successful breeding in the first year of life. Other hummingbird species with similar timing to the second and definitive prebasic molts may show similar high annual survivorship.

Additionally, species with an advanced timing to the second prebasic molt replace fewer greater coverts in the preformative molt than do species with similar timing to the second and definitive prebasic molts. In most avian families, more extensive molts are correlated with increased solar exposure and habitat abrasiveness (Pyle 1998, Pyle 2008, Carnes et al. 2021b, Guallar et al. 2021, Pyle and Carnes 2022); however, hummingbird species in this study with similar timing to the second and definitive prebasic molts and more extensive preformative molts are regularly species of forest understory, with limited solar exposure, while species with an advanced second prebasic molt are all species of forest canopy, forest edge, and open habitats (Billerman et al. 2022), which have greater solar exposure. Because feathers are on the body for less than a calendar year in species with an advanced second prebasic molt, there may be less need for these species to replace juvenile greater coverts in the preformative molt than there is for species with similar timing to the second and definitive prebasic molts.

Bill corrugations were reduced or absent after first-cycle formative plumage in all 19 species, similar to temperate North American species and other tropical species (Stiles and Wolf 1974, Yanega et al. 1997, Carnes et al. 2021a, Pyle 2022b), providing a useful age criteria in situations where molt limits are difficult to detect, such as photographs in which harsh lighting washes out the iridescent quality of replaced feathers. Assuming consistent rates of bill smoothing over a period of 5–9 months in most species, the presence of corrugations in photos of some individuals undergoing the second prebasic molt in species with an advanced timing to this molt suggests that extensive corrugations on definitive-cycle basic individuals may indicate that the bird is in second-cycle basic plumage. It is also possible that some definitive-cycle basic individuals may keep a small degree of corrugations for the entire lifespan, as in some North American species (Yanega et al. 1997, Pyle 2022b). Similarly, in species with sexual dichromatism to the bill, definitive-cycle basic males with less-extensive areas of bright color likely indicate a bird in second-cycle basic plumage, as in some species of the southwestern United States such as in the genera *Cynanthus*, *Basilenna*, *Leucolia*, and *Amazilia* (Pyle 2022a).

Males of all species with sexual dichromatism showed delayed maturation in their plumage and/or bill characteristics and did not achieve full male-like characteristics until at least the second prebasic molt, similar to the delayed maturation of male hummingbirds in other regions (Carnes et al. 2021a, Pyle 2022a). In addition to the dramatic degree of sexual dichromatism present in some of our study species (e.g., Black-crested Coquette, Violet Sabrewing, Crowned Woodnymph), others (e.g., Buff-bellied Hummingbird, Rufous-tailed Hummingbird) show a more cryptic degree of dichromatism, with differences present in the bill coloration and patterning, and the plumage of the head and throat. Minor sex-based differences in coloration and patterning should be looked for in hummingbird species that are currently thought to be monochromatic. In White-necked Jacobin and Green-breasted Mango, which both have significant sexual dichromatism, some definitive-cycle basic females exhibited male-like body plumage. True polymorphism appears to be rare in female hummingbirds, with definitive evidence for this trait only in White-necked Jacobin and rare individuals in *Anthracothorax* (Clark et al. 2022). The first-cycle juvenile plumage of White-necked Jacobin is similar to the definitive-cycle basic plumage in males, and first-cycle females and definitive-cycle basic females of the male-like "blue" morph are found to experience less social aggression than definitive-cycle basic females of the "speckle-throated" morph; plumage type in this species appears to remain set after the second prebasic molt (Bleiweiss 1985, Falk et al. 2021). Unlike White-necked Jacobin, which shows a male-like plumage in juvenile and first-cycle formative plumages, Green-breasted Mango has a more female-like plumage in these plumages, meaning that only older females obtain male-like plumage, similar to older females in other strongly sexually dichromatic tropical birds such as manakins (Doucet et al. 2007, Scholer et al. 2022), which may be the result of altered hormone levels (Kimball and Ligon 1999). Different selective pressures likely affect the development of male-like plumage in females of White-necked Jacobin and Green-breasted Mango.

Photographic collections tend to be biased toward unusual and visually appealing individuals (Zbyryt et al. 2021, Pyle 2022a), and we encourage those contributing images to the Macaulay Library and eBird to include birds of all age and sex classes, and of birds in molt or worn plumages. Definitive-cycle basic males and females with male-like plumage, which are more visually appealing to many photographers, made up 56.1% of the images in our study species with easily discernable sexual dichromatism, with one species (Violet Sabrewing) as high as 80.2%. Also, overall sample sizes were small for species that do not frequent feeders and/or prefer dimly-lit forest understory habitats, and relatively few photographs were available of birds in active molt. These biases for sex, behavior, and appearance, along with higher image totals by month for the November–March period, which is the busiest portion of the year for tourism in the study region, suggests that Macaulay Library imagery from tropical regions may currently be biased by patterns of bird watcher behavior. This could be offset by encouraging photographic contributions from local birders throughout the annual cycle. Additionally, researchers using imagery from photographic libraries such as the Macaulay Library must be aware of limitations, including at least a small proportion of misidentified photos, numerous low-quality images, and relatively few photos showing birds in positions that allow for analysis.

Mark-recapture programs using appropriate-sized bands could further elucidate the progression of plumages on an individual basis, show the exact timing of delayed maturation, and reveal rates of females with male-like plumage characteristics. Additional banding studies will likely show minor differences with our data, especially in regard to bill corrugations by age and molt extent in species that rarely replace greater coverts, and could show if there are any variations in these characteristics within species with large geographic ranges. Most species in our study were not undergoing molt during the MoSI time frame, and banding efforts occurring in other portions of the annual cycle could obtain larger samples of molt and draw a better picture of molt timing in relation to breeding.

Further efforts are necessary to determine if males of species with an advanced timing to the second prebasic molt produce mechanical sounds or have reduced survivorship in comparison to females, as in North American species of the Bee clade (Calder et al. 1983, Mulvihill et al. 1992). Additionally, although photographs of females on nests are difficult to evaluate, all such individuals that we were able to age appeared to be in definitive-cycle basic plumage, implying that these hummingbird species do not breed prior to the second prebasic molt. Pyle (2022a) suggested that in one species with an advanced second prebasic molt (Violet-crowned Hummingbird, *Leucolia violiceps*), second-cycle basic individuals could attempt breeding after the breeding period of older individuals. Further study is needed to determine age at first breeding in these and other hummingbird species, and if there is differential individual timing to breeding according to age.

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Data Availability:

The data/code that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.3ffbg79nf. The Belize Forestry Department granted permits for conducting research within Belize. This research was conducted in compliance with the Guidelines to the Use of Wild Birds in Research and with the ethics standards of the North American Banding Council.

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Supplemental Materials for:

Many Central American hummingbirds can be aged and sexed by molt patterns and bill corrugations

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Acknowledgements

Table S1. Molt, plumage, and bill coloration ageing and sexing criteria for nineteen species of Central American hummingbirds. Preformative molt extent partial, and prebasic molt extent complete in all species. Information on presence/absence and degree of sexual dichromatism from Birds of the World accounts (Billerman et al. 2020) and Fagan and Komar (2016).

Species	Clade	N	Molt limits in FCF	DCB bill corrugations (maximum %)	Sexual dichromatism (presence/absence or degree)	Delayed plumage/bill color maturation in males?
White-necked Jacobin	Topaz	133	Between primary and greater coverts, or within greater coverts	0% (N = 101)	Major, but a minority of DCB females show male-like plumage	Yes. FCF males retain juvenile tail pattern until SPB.
Band-tailed Barbthroat	Hermit	72	Between primary and greater coverts, or within greater coverts	0% (N = 43)	Negligible. Potential difference in coloration of underside.	No.
Long-billed Hermit	Hermit	62	Within greater coverts, or between primary and greater coverts	0% (N = 13)	None.	No.
Stripe-throated Hermit	Hermit	68	Between primary and greater coverts, or within greater coverts	5% (N = 36)	Slight. Potential difference in rectrix shape.	No.
Brown Violetear	Mango	137	Between median and greater coverts	0% (N = 43)	None.	No.
Purple-crowned Fairy	Mango	114	Between median and greater coverts, or between primary and greater coverts	0% (N = 42)	Moderate. DCB males with iridescent purple crown, tail with different pattern and shorter length.	Yes. FCF males retain intermediate tail pattern until SPB, and may retain brown feathers in crown.
Green-breasted Mango	Mango	224	Between median and greater coverts, or within primary coverts	0% (N = 103)	Major. DCB males with green body, dark stripe on breast. Female with dark stripe on white underside. Some DCB females with male-like body plumage.	Yes. FCF males with juvenile-like body plumage.
Black-crested Coquette	Coquette	150	Between median and greater coverts	0% (N = 104)	Major. DCB male with thin black plumes around iridescent patches on crown and throat, and red bill. Female with white throat and black on upper mandible.	Yes. FCF males without plumes and iridescent patches on head, and bill with red only at base of upper mandible.

Canivet's Emerald	Emerald Group A	141	Between median and greater coverts	0% (N = 76)	Major. DCB male entirely iridescent green, with deeply forked tail and red bill. Female with white underside and black upper mandible.	Yes. FCF males with incomplete iridescence, upper mandible black.
Wedge-tailed Sabrewing	Emerald Group B	136	Within greater coverts or between primary and greater coverts	0% (N = 64)	Minor. DCB males with white tips to rectrices, modified rachides in outer primaries.	Yes. FCF males retain unmodified juvenile primaries, have narrower rectrices with less white.
Violet Sabrewing	Emerald Group B	105	Between median and greater coverts, or within greater coverts	0% (N = 90)	Complete. DCB males iridescent violet and green with modified rachides in outer primaries, females with green backs, gray belly, some iridescence in throat.	Yes. FCF males with incomplete iridescence, no modifed outer primaries.
Stripe-tailed Hummingbird	Emerald Group C	64	Between median and greater coverts	0% (N = 21)	Partial. Male with iridescent green on throat, breast, and belly, female grayish white below.	Yes. FCF males with incomplete iridescence.
Crowned Woodnymph	Emerald Group C	76	Within greater coverts or between median and greater coverts.	0% (N = 48)	Complete. Male entirely iridescent, with purple crown, breast, and belly, green head, throat, and back, and forked blue tail. Female green above and gray below.	Yes. FCF males with incomplete iridescence.
Scaly-breasted Hummingbird	Emerald Group D	84	Between median and greater coverts	0% (N = 24)	Minor. DCB males with modified rachides in outer primaries.	Yes. FCF males retain unmodified juvenile primaries
Azure-crowned Hummingbird	Emerald Group D	178	Between median and greater coverts	0% (N = 79)	Negligible. Potential difference in brightness of crown color.	No.
Cinnamon Hummingbird	Emerald Group D	168	Between median and greater coverts	0% (N = 78)	Minor. DCB males with extensive pink on upper mandible,	Yes. FCF males with mixed pink and black coloration on mandible.
Buff-bellied Hummingbird	Emerald Group D	59	Between median and greater coverts	0% (N = 17)	Minor. DCB males with extensive red on upper mandible.	Yes. FCF males with mixed red and black on mandible.
Rufous-tailed Hummingbird	Emerald Group D	290	Between median and greater coverts	10% (N = 85)	Minor. DCB males with extensive red on upper mandible, iridescent green gorget; DCB females with limited red mandible, "frosted" gorget.	Yes. FCF males with limited red on mandible and "frosted" gorget.
White-bellied Emerald	Emerald Group D	170	Between median and greater coverts	10% (N = 67)	None.	No.

Figures S1-S19. Images of 19 Central American Hummingbird Species exemplifying different molts and plumages, showing age and sex criteria.

These images focus on showing differences between formative and definitive plumage, and all species include at least 2 images. In some species, rather than an individual in formative plumage, an individual partially through the second prebasic molt but still showing a molt limit is included, and for Band-tailed Barbthroat, which had a low number of presentable images in the ML, we show an individual in juvenile plumage rather than an individual in formative plumage. For species with sexual dichromatism we show images of both males and females for the ages at which sexes are discernible.

For images used by permission from the Cornell Laboratory of Ornithology's Macaulay Library, the Macaulay Library catalogue number for each image ("ML" followed by 8 or 9 numbers) follows the text and includes a link to the page for the image. These pages include information on date, location, and photographer, as well as links to the respective eBird checklist for which the photo was contributed.

Figure S1. Images exemplifying molts and plumages in White-necked Jacobin

FPF. Note buffy malar stripe and turquoise-blue head feathering (contrasting with deep blue of the actively molting throat). Molt limit between dull brown-green greater coverts and metallic green median coverts. ML 190568541

SPB of unknown sex. Note actively molting primaries (with remaining older primaries quite worn and frayed at the tips) contrast between worn, dull juvenile greater coverts and deep green formative median coverts, and broad blue edging and gray interior of central rectrices. ML 134566741

SPB female molting into "speckle-throated" basic plumage. Note actively molting outer primaries and remaining blue feathers in the throat. ML 95185891

DCB female "speckle-throated" morph. Note lack of contrast between greater and median coverts. ML 171030221

DCB male. Note rectrices almost entirely white with thin blue edging, and lack of contrast between greater and median coverts. [ML 240480861]

Figure S2. Images exemplifying molts and plumages in Band-tailed Barbthroat

FCJ. Note pale buff edging to most feathers. ML 193782571

DCB. Note lack of molt limits within wing. ML 156492471

Figure S3. Images exemplifying molts and plumages in Long-billed Hermit

FCF. Note pale tips to retained outer juvenile greater coverts. ML 317168681

DCB. Note lack of contrast between greater and median coverts. ML 290028221

Figure S4. Images exemplifying molts and plumages in Stripe-throated Hermit

FCF. Note worn and dull retained juvenile outer greater coverts and worn tail. ML 211747861

DCB. Note lack of contrast within wing feathers. ML 389910811

Figure S5. Images exemplifying molts and plumages in Brown Violetear

FCF. Note buff tips to greater coverts. ML 383572291

DPB. Note lack of tipping on the retained greater coverts. ML 279961321

Figure S6. Images exemplifying molts and plumages in Purple-crowned Fairy

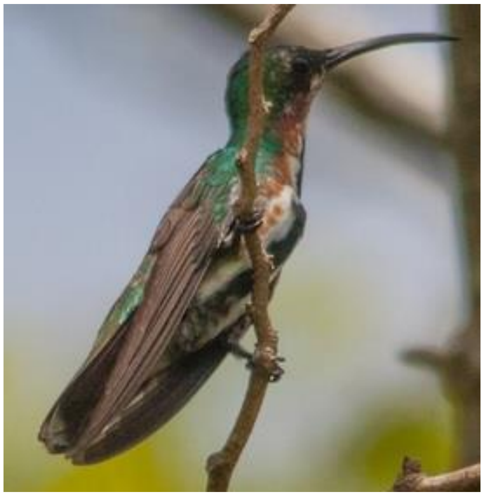
FCF male. Note brown feathers in the cap and sides of the head, and slight contrast in color between the formative median coverts and juvenile greater coverts. ML 228153981

SPB female. Note significant wear and color contrast in the remaining inner juvenile greater coverts versus the formative median coverts. Significant wear to the remiges as well. ML 279582971

DCB female. Note lack of contrast within the wing. ML 409133341

DCB male. Note lack of contrast within the wing and complete adult head pattern. ML 400234081

Figure S7. Images exemplifying molts and plumages in Green-breasted Mango



FCF. Note contrast in wear and color between the juvenile greater coverts and formative median coverts. ML 62100661

DCB female with typical plumage. Note lack of contrast within the wing. ML 408096031

DCB female with male-like body plumage on a nest. ML 218729461

DCB male. Note lack of contrast within the wing. ML 142975861

Figure S8. Images exemplifying molts and plumages in Black-crested Coquette

FCF male. Note contrast in color and wear between the juvenile greater coverts and formative median coverts, mixed bill color, and dark throat. ML 156059641

FCF female. Note contrast in color and wear between the juvenile greater coverts and formative median coverts, and dark upper mandible. ML 338778121

DCB female. Note lack of contrast in the wing and mixed bill color. ML 23625071

DCB male. Note lack of contrast in the wing, red bill, and full male-like appearance in the feathering of the head. ML 383553521

Figure S9. Images exemplifying molts and plumages in Canivet's Emerald

FCF male. Note dark upper mandible and patchy iridescence on the breast and throat. ML 235634071

SPB female. Note contrast in color and wear between the median coverts and two formative inner greater coverts versus the juvenile outer greater coverts. Additionally, significant wear to the remaining juvenile remiges. ML 246035701

SPB male. Note contrast in color and wear between the formative median coverts and juvenile greater coverts, and the dark bill. Patchy iridescence on throat and breast as in FCF. ML 253587301

DCB female. Note lack of contrast within the wing. ML 289383721

DCB male. Note lack of contrast in the wing, red bill with black tip, and complete iridescence. ML 47817731

Figure S10. Images exemplifying molts and plumages in Wedge-tailed Sabrewing

FCF. Note contrast in color between formative median coverts and inner two greater coverts versus the juvenile outer greater coverts and remiges. ML 327685111

DCB female. Note lack of contrast within the wing. Rachides of outer primaries not modified. ML 119482111

DCB male. Note lack of contrast in the wing and modified rachides to the outer primaries. ML 191469471

Figure S11. Images exemplifying molts and plumages in Violet Sabrewing

FCF male. Note partial iridescence to body plumage, contrast in wear and color between the juvenile greater coverts and formative median coverts, and unmodified rachides to outer primaries. ML 377108631

FCF female. Note contrast in color and wear between the formative median coverts and inner three greater coverts, versus the juvenile outer greater coverts and remiges. ML 398967551

DCB female. Note lack of contrast within the wing. ML 124712951

DCB male. Note completely iridescent body plumage, lack of contrast within the wing, and modified rachides to the outer primaries. ML 200412261

Figure S12. Images exemplifying molts and plumages in Stripe-tailed Hummingbird

FCF male. Note iridescence on the underside confined to the gorget. Wing criteria as in FCF females. [ML 141626641](https://macaulaylibrary.org/asset/141626641)

FCF female. Note contrast in color and wear between the formative median coverts and inner two greater coverts versus the juvenile outer greater coverts. [ML 34208931](https://macaulaylibrary.org/asset/34208931)

DCB female. Note lack of contrast within the wing. [ML 161154401](https://macaulaylibrary.org/asset/161154401)

DCB male. Note lack of contrast within the wing, complete iridescence of body plumage. [ML 363305151](https://macaulaylibrary.org/asset/363305151)

Figure S13. Images exemplifying molts and plumages in Crowned Woodnymph

FCF male. Note incomplete iridescence to underside. Wing criteria as in FCF female. ML 171325891

FCF female. Note contrast in color and wear between juvenile greater coverts and formative median coverts. ML 93329261

DCB female. Note lack of contrast in the wing. ML 92381241

DCB male. Note lack of contrast in the wing and complete iridescence to the gorget. ML 304572151

Figure S14. Images exemplifying molts and plumages in Scaly-breasted Hummingbird

FCF. Note contrast in color and wear between the formative median coverts and juvenile greater coverts, which have pale tips. No modification to rachides of outer primaries. ML 91132441

DCB female. Note lack of contrast in the wing and unmodified rachides in outer primaries. ML 213735061

DCB male. Note lack of contrast in the wing and modified rachides to the outer primaries. ML 350480691

Figure S15. Images exemplifying molts and plumages in Azure-crowned Hummingbird

FCF. Note contrast in color and wear between the formative median coverts and juvenile greater coverts. ML 228071781

DCB. Note lack of contrast in the wing. ML 384046131

Figure S16. Images exemplifying molts and plumages in Cinnamon Hummingbird

FCF. Note contrast in color and wear between the formative median coverts and juvenile greater coverts. Significant wear to the juvenile remiges and coverts. Upper mandible with some dark coloration in the outer third and black line along edge. ML 87300961

DCB female. Note lack of contrast in the wing, upper mandible mostly pink with black along outer edge. ML 166138671

DCB male. Note lack of contrast in the wing, upper mandible pink with black tip. ML 125567581

Figure S17. Images exemplifying molts and plumages in Buff-bellied Hummingbird

FCF male. Note contrast in color and wear between the formative median coverts and juvenile greater coverts. Upper mandible mostly red, but with black line along outer edge. Gorget with some pale tipping. ML 408952211

FCF female. Note contrast in color and wear between the formative median coverts and juvenile greater coverts. Upper mandible mostly dark. ML 336914131

DCB female. Note lack of contrast in the wing, upper mandible mostly red but with black line along outer edge, gorget with pale tipping. ML 118561121

DCB male. Note lack of contrast in the wing, upper mandible red with black tip, gorget with minimal pale tips. ML 288795691

Figure S18. Images exemplifying molts and plumages in Rufous-tailed Hummingbird

FCF male. Note contrast in color and wear between formative median coverts and juvenile greater coverts. Upper mandible mostly dark. Gorget with frosted appearance. ML 395001481

FCF female. Note contrast in color and wear between formative median coverts and juvenile greater coverts. Upper mandible black. ML 81726791

DCB female. Note lack of contrast within the wing. Upper mandible mostly dark. Gorget with frosted appearance. ML 223643881

DCB male. Wing criteria as in DCB female. Upper mandible mostly red, with black along outer edge. Gorget without pale tips. Photo from MoSI banding data.

Figure S19. Images exemplifying molts and plumages in White-bellied Emerald

FCF. Note contrast in color and wear between the formative median coverts and juvenile greater coverts. ML 367646701

DCB. Note lack of contrast in the wing. ML 167833551

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