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SHORT NOTE

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A FEMALE-LIKE, DEFINITIVE ALTERNATE PLUMAGE IN MALE BEE HUMMINGBIRDS *MELLISUGA HELENAE*

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Abstract · Adult hummingbirds were formerly thought to undergo only a single prebasic molt per year, but prealternate molts have recently been documented that may or may not include the bright and iridescent feathers of males. I examined 2,738 images of the Bee Hummingbird *Mellisuga helenae* at the Macaulay Library. Among images of 653 males and 135 females, I documented prealternate molt occurring in adults, during which the iridescent red gorget feathers of males were completely replaced with non-iridescent feathers in July-September and replaced again with iridescent feathers in December-January. Molt of flight feathers occurred in October-December. I defend a terminology whereby the first replacement of body feathers is part of a definitive prealternate molt. I further suggest that cryptic coloration due to loss of the gorget feathers may have evolved for predation avoidance or reduction of territorial disputes during a vulnerable period in which primaries are being replaced.

Resumen · Anteriormente se creía que los colibríes adultos experimentaban una sola muda prebásica al año, pero recientemente se han documentado mudas prealternas que pueden o no incluir las plumas brillantes e iridiscentes de los machos. Examiné 2.738 imágenes del colibrí abeja *Mellisuga helenae* en Macaulay Library. De las imágenes de 653 machos y 135 hembras, documenté la muda prealterna en adultos, donde las plumas de la gorguera de los machos se reemplazaron completamente por plumas no iridiscentes entre julio y septiembre, y nuevamente por plumas iridiscentes entre diciembre y enero. La muda de las plumas de vuelo ocurrió entre octubre y diciembre. Defiendo una terminología según la cual el primer reemplazo de las plumas corporales forma parte de una muda prealterna definitiva. Sugiero además que la coloración críptica debido a la pérdida de las plumas de la garganta puede haber evolucionado para evitar a los depredadores o reducir las disputas territoriales durante un período vulnerable en el que se están reemplazando las plumas primarias.

Key words: *feather production · follicle · hummingbird · molt and plumage cycles · prealternate molt*

INTRODUCTION

Among species of birds, all "adults" (defined here as ca. ≥ 1 year of age) typically undergo a single annual prebasic molt that is complete or nearly so, whereas a smaller proportion of species can undergo a second, prealternate molt that is less than complete (Howell et al. 2003, Pyle 2008, 2022a; Johnson and Wolfe 2018). The resulting alternate plumage can be similar in color and pattern to the basic plumage, can be showier or brighter than the basic plumage, especially in males, or can be more cryptic than the basic plumage, providing camouflage during replacement of flight feathers. The last strategy appears to be employed by ptarmigan and some ducks (Pyle 2005, 2007).

Formerly, adult hummingbirds were thought to undergo only a single prebasic molt per year (Pyle et al. 1997). Recently, however, prealternate molts have been documented in the bee tribe (Mellisugini) that may or may not include the bright and iridescent gorget or other metallic feathers of males (Dittmann and Cardiff 2009, Sieburth and Pyle 2018, Clark et al. 2024). The Bee Hummingbird *Mellisuga helenae* is endemic to Cuba, is noted for being the smallest bird in the world, and breeds primarily in March-July (Schuchmann 1999, Kirkconnell and Garrido 2024, Mugica Valdes et al. 2025).

Kirkconnell and Garrido (2024) noted that adult male Bee Hummingbirds have a "non-breeding" plumage that resembles females, suggesting that a prealternate molt occurs, but our understanding of molt and plumage sequences in this species is lacking. Here, I aimed to document the molt and plumage cycles of the Bee Hummingbird and compare them to those of other hummingbirds that undergo prealternate molts. I then relate results to interpretations of molt and plumage strategies and terminology in hummingbirds, and suggest that cryptic coloration resulting from the loss of the gorget feathers may have evolved for predation avoidance and/or reduction of territorial disputes.

METHODS

This analysis was based on examination of 2,738 images catalogued at the Cornell Lab of Ornithology's Macaulay Library (see Pyle 2022b and Clark et al. 2024 for use of this catalogue to study molt in hummingbirds). I examined all images uploaded as of 20 July 2025

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(indicated below by ML number), ordered from oldest to newest date of observation, and only included one datum per date, location, and plumage category, to reduce sampling the same bird more than once (Pyle 2022b). During this examination, I confirmed the information in Kirkconnell and Garrido (2024) that adult females differed from adult males by having broad white tips to the outer two rectrices, lacking in adult males. Adult males also differed from females by having brighter and deeper blue (less greenish blue to bluish green) upperparts and central rectrices, more extensive metallic green-blue feathering on the sides of the underparts, and dusky centers to undertail coverts. Careful examination of images revealed that juveniles and first-year birds (see below for ageing) also showed these sex-specific differences, except that some (but not all) males could have white tips to the juvenile outer rectrices (if present, usually narrower than in juvenile and first-year females). Within each sex the upperparts of juveniles also averaged duller than those of adults, and in all age/sex groups the upperparts averaged duller and greener with feather wear. These age and sex differences accord with those of North American hummingbirds of the bee clade (Pyle 2022a) and have also been detailed in Mugica Valdes et al. (2025). When visible, I used the presence and extent of corrugations at the base of the culmen to age birds (Yanega et al. 1997, Pyle 2022a); see examples in Figures 1c, ML95971861, and ML620386484 (absent), and Figures 2a, 2b, ML329456851, ML185296401, and ML329456781 (present). I concluded that a limited preformative molt was present in the first cycle, as defined for other small gorgeted hummingbirds by Pyle (2022a), allowing further separation of first-cycle birds from adults by mixed juvenile and formative upperpart feathers and upper wing secondary coverts, and by weaker and more worn juvenile flight feathers (Pyle 2022a, 2022b; see examples in Figures 2c–2e). I aged birds broadly as first-cycle (≤1 year of age), second-cycle (replacing juvenile primaries), and adult.

My detailed analysis was confined primarily to males, using the sex-determination criteria summarized above, although I also assessed molts and plumages in females when possible. Images not showing sex-specific characters were excluded whereas all images of the same individual within a checklist were examined to inspect as much of the plumage characters as possible. I categorized each male as 1) fully gorgeted with iridescent red throat and crown feathers (Figure 1a), 2) molting gorget feathers (Figure 1a and 1e), or 3) lacking any iridescent red feathers to the throat and crown (Figure 1c and 1d). Birds categorized as molting contained at least three pin feathers to avoid including those with adventitious feather replacement. I also categorized whether or not females and males were undergoing active molt of primaries (Figure 2d). Data were binned by month of observation for analysis. Temporal ranges for body feather molts were estimated using mean + 1.96 SD on Julian dates, and for molt of primaries using the models suggested by Underhill and Zucchini (1988) and Scott and Underhill (2024).

RESULTS

Of the 2,738 images examined, I obtained samples of 653 individual males and 135 individual females, considering only one datum per date, location, and plumage category. Sample sizes of individual males per month ranged from only five taken in September to 156 taken in March. Of the 653 males, 433 were considered fully gorgeted (Figure 1a), 117 were molting

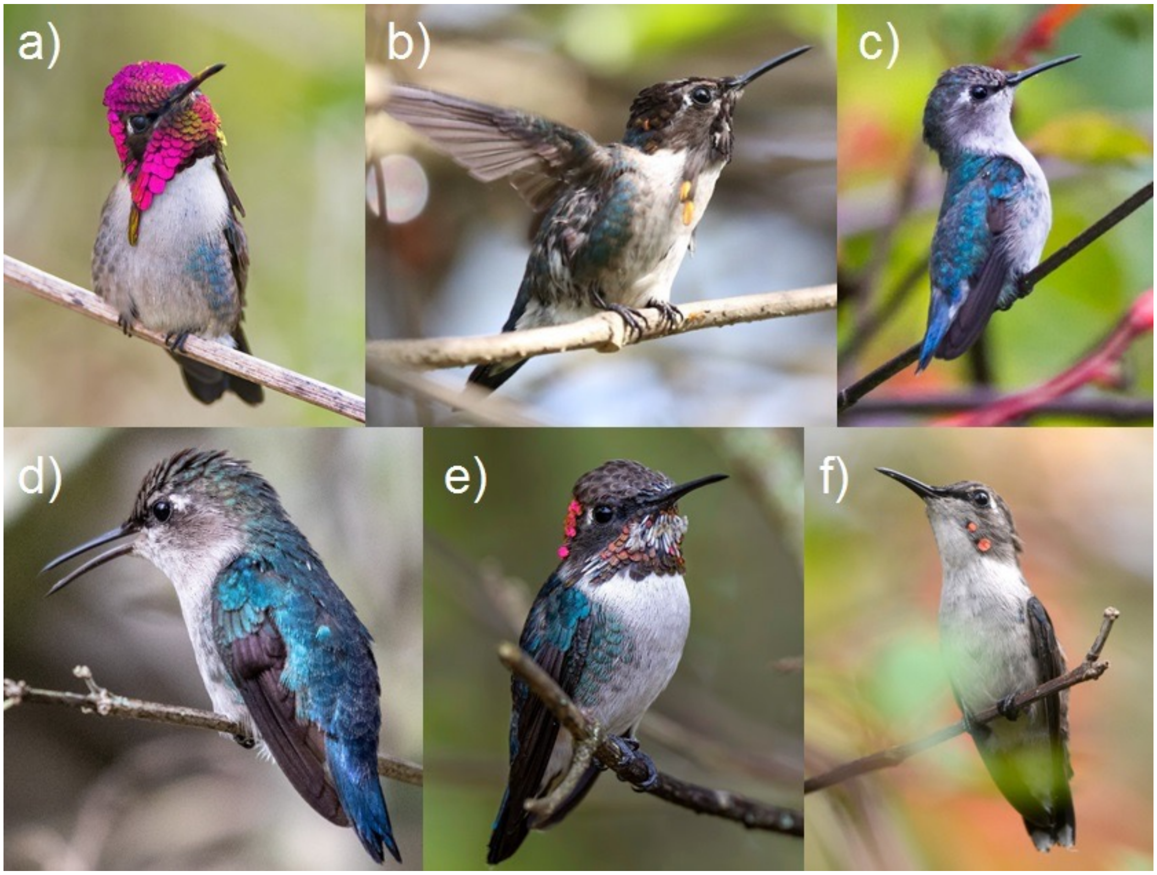

Figure 1. Examples of adult (≥ 1 year old) male and female Bee Hummingbirds *Mellisuga helenae* from Cuba exhibiting definitive plumages and molts through an annual cycle. a) full-gorgeted male in basic plumage, 26 March 2010; b) male undergoing prealternate molt of worn gorget feathers, 14 July 2018; c) male with alternate crown and throat feathering while commencing prebasic molt of primaries, 6 October 2019; d) male with alternate crown and throat feathering having completed prebasic primary molt, 10 November 2019; e) male completing prebasic molt of gorget feathers 23 December 2022; f) female in alternate plumage with iridescent throat feathers, 18 October 2017. Photos cropped for enlarged presentation and used by license agreement from the Macaulay Library © Kevin Elsby (a, ML388004011), Megan Digeon (b, ML 307292381), Vladimir Mirabal (c, ML345529711), Steve McInnis (d, ML188600601), Su Li (e, ML520396141), and Nikolaj Mølgaard Thomsen (f, ML73180681).

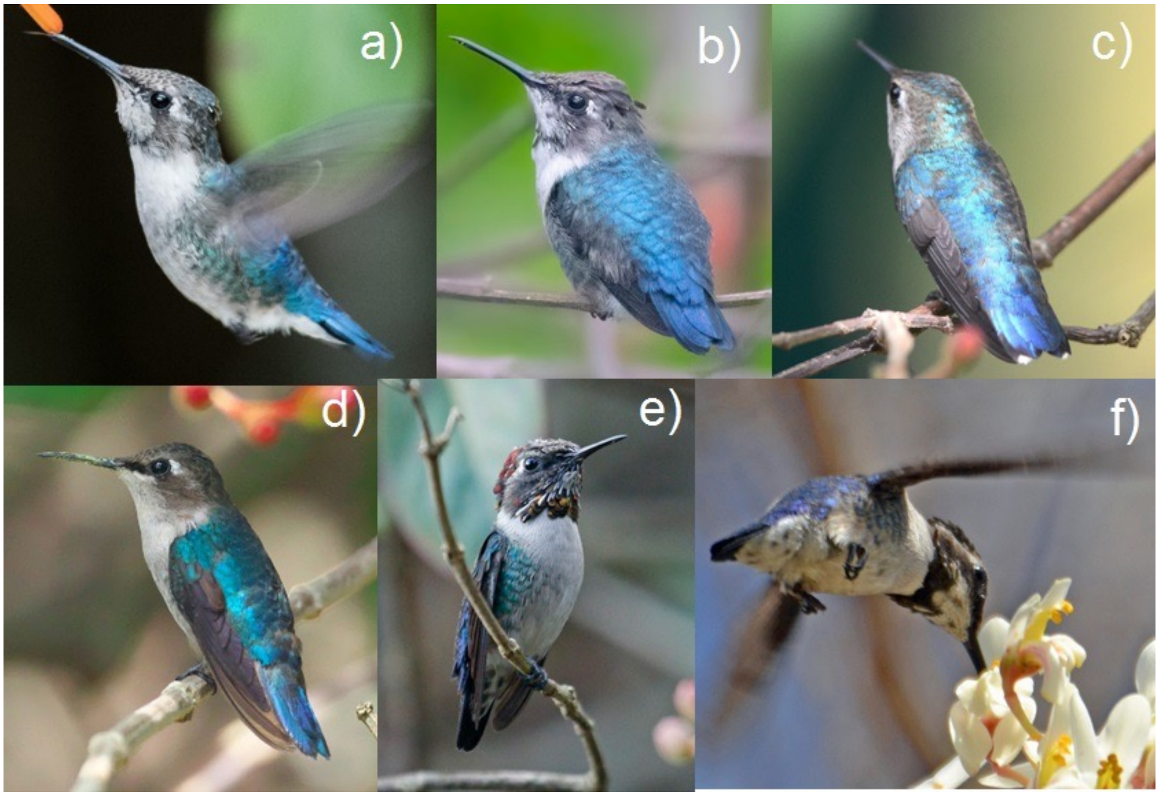

Figure 2. Examples of male Bee Hummingbirds *Mellisuga helenae* from Cuba during the first and second molt cycles. a) juvenile plumage, 20 March 2017; b) undergoing preformative molt during the first molt cycle (cf. Pyle 2022a) including the development of incoming iridescent gorget feathers, 3 May 2023; c) formative plumage during the first cycle including mixed juvenile and formative back feathers and upperwing coverts, along with narrow white tips to the juvenile rectrices found in some males, 18 October 2017; d) male undergoing second prebasic molt of juvenile primaries (cf. Pyle 2022b), 15 February 2017; e) male presumably undergoing second prebasic molt of gorget feathers based on the late date, 1 March 2019; f) second basic plumage with incomplete gorget in a bird that appears to have undergone an incomplete second prebasic molt, 16 April 2017. Photos cropped for enlarged presentation and used by license agreement from the Macaulay Library © R. Dennis Ringer (a, ML55257701), Jo Hofmann (b, ML622051932), Nikolaj Mølgaard Thomsen (c, ML73180651), Paul Tavares (d, ML51475771), Adam Bowley (e, ML205391781), and Michale J. Good (f, ML56417381).

gorget feathers (Figure 1b), and 103 contained no molting or iridescent red feathers to the throat and crown (Figure 1d).

Thirty-nine birds actively molting primaries included 16 females and 23 males. Dates for these ranged from 6 October (Figure 1c) to 15 February (Figure 2d), and the Underhill-Zucchini model suggested a temporal range of 1 October to 22 February for molt of juvenile and basic primaries combined. For birds in molt that could be aged with confidence, replacement of basic primaries (N = 12) occurred from 6 October (Figure 1c) to 25 December (ML197500061, ML 211351791) and replacement of juvenile primaries (N = 7) occurred from 6 December (ML270498151) to 15 February (Figure 2d). Underhill-Zucchini models estimated these date ranges as 29 September to 26 December and 17 November to 28 February, respectively, but caution should be applied due to low sample sizes. All 23 of the males molting primaries completely lacked red iridescent feathers in the crown and throat (Figures 1c–d and 2c–d).

Proportions of males with full gorgets, molting gorget feathers, and no red gorget feathers are shown in Figure 3. Males with full red gorgets (Figure 1a) ranged in date from 20 November (ML611495304) to 3 September (ML483679671) or 21 November to 14 September using mean ± 1.96 SD. Several males scored as completely gorgetted in late December-March had not completed growth of the elongated iridescent feathers on the sides of the throat (e.g., ML613910187, and ML620834118), indicating that growth of these feathers extended beyond replacement and full development of other iridescent throat feathers.

Adult males with no red feathers in the crown and throat (Figures 1c–d) ranged from 30 July (ML598940621) to 7 January (ML526067061) or 26 July to 7 January (mean + 1.96 SD) and included 13 birds prior to primary molt and 17 males during primary molt (e.g., Figure 1c). Twenty-two first-cycle males continued to lack iridescent feathers for the most part (Figures 2c and 2d), with one exception (Figure 2b; see below), and included 16 birds prior to molt of primaries and six birds during primary molt. Given this wide temporal age-specific difference, I assumed that 10 fully-gorgetted males that had completed primary molt (and thus could not be aged) from 10 November (Figure 1d) to 19 January (ML545755091) were adults, and that six males without iridescence having completed primary molt from 5 February (ML243206441) to 7 March (ML474455881) were first-cycle birds, but confirmation of this may be needed. No male of either age group or unknown in age showed red iridescent feathers in October (Figure 3), and 60 of 62 non-molting males in September-November lacked red. Interestingly, however, three females during this period (as identified by white-tipped rectrices and the other sexing criteria noted above) did show one to a few iridescent feathers in the crown and/or throat during 5 September to 8 November (Figure 1f; ML38199191, ML40634981).

Males molting gorget feathers were separated into two groups, those replacing iridescent with non-iridescent feathers in early July to mid-September and those replacing non-iridescent with iridescent feathers from late October to mid-April (Figure 3). Nine adult males in the first group were recorded from 14 July (Figure 1b) to 3 September (ML483679641), or 7 July to 16 September (mean + 1.96 SD), although the sample size for the latter calculation was low (Figure 3). Examination of the 105 males and 33 females in the ensuing plumage (lacking iridescent feathers) indicated that scattered upperpart and underpart feathers were also replaced during this molt in both males (e.g., Figure 2c and ML183920851, ML42873931, ML205135321,

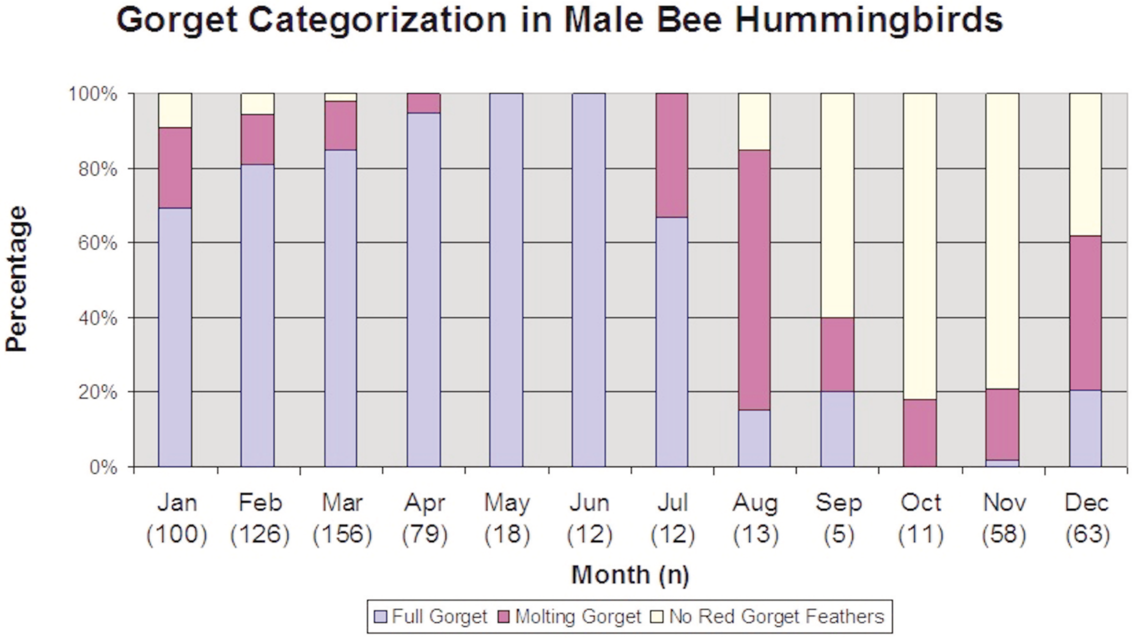

Figure 3. Percentages of male Bee Hummingbirds *Mellisuga helenae* in three plumage categories (fully red-gorgeted, molting gorget feathers, and lacking iridescent red gorget feathers) by month. Sample sizes of individual males are in parentheses below each month.

627546853) and females (e.g., ML611264036, ML224399741 along with those with iridescent feathers referenced above).

The remaining males replacing non-iridescent with iridescent gorget feathers (Figures 1e and 3e) were recorded from 31 October (ML621698359) to 16 April (Figure 1f, Figure 3), or 6 November to 20 March (mean + 1.96 SD). Because flight-feathers had been replaced, these males could not be aged, but based on the differing temporal periods of flight-feather molt by age, as described above, it was presumed that adults molted in iridescent gorget feathers primarily in December-January whereas second-cycle birds replacing or having replaced juvenile primaries molted in iridescent gorget feathers primarily in February-April, and it follows that males with shorter elongated gorget feathers to the sides of the throat in late December-January were adults whereas those showing this feature in March-April were second-cycle birds, but this may require confirmation. The temporal gap between the mean dates of of gorget-feather replacement (12 August, based on mean + 1.96 S.D.) and peak primary molt (12 December, based on the Underhill-Zucchini-Underhill model), 122 days, was much larger than that between peak molt and the mean date for growth of gorget feathers (12 January), 31 days.

Some second-cycle males of North American Hummingbirds may be identifiable by weak or incomplete gorgets in basic plumage (Pyle et al. 1997, Pyle 2022a). Other than the bird in Figure 3f, however, no other males showed incomplete gorgets; thus, the proportion of second-cycle male Bee Hummingbirds in this category appears to be small at best.

Seventeen juveniles (Figure 2a) of both sexes were recorded from 16 March (female, ML317503911) to 2 August (male, ML622609673), and 28 first-cycle birds of both sexes undergoing preformative molt or in formative plumage (Figure 2c) were recorded from 3 May (male, Figure 2b) to 17 November (male, ML628418749). Very few first-cycle males showed scattered, formative, iridescent feathers as shown by *Calypte*, *Selasphorus*, and other related hummingbirds (Pyle 2022a), the male molting on 3 May (Figure 2b) being an apparent exception. I could not determine from the images if two inserted molts (preformative and first prealternate) occurred during the first cycle; a first prealternate molt has thus far not been documented in hummingbirds (Pyle 2022a).

DISCUSSION

I confirmed the indication by Kirkconnell and Garrido (2024) that adult Bee Hummingbirds undergo an inserted prealternate molt, both sexes molting at least feathers of the head and throat, as well as other scattered body feathers, twice per adult (definitive) molt cycle. Males completely replaced iridescent gorget feathers with non-iridescent feathers in July–September and replaced them again with iridescent feathers in November-January. Molt of primaries, secondaries, and rectrices in adults occurred in October–December, in between these two body-feather molts. First-cycle birds underwent a preformative molt in May until (perhaps) August, and most of these males did not gain iridescent feathers until February-April, following the second prebasic molt of primaries in December-February.

Two interpretations have been proposed for molt terminology in hummingbirds that include a definitive prealternate molt, depending on which replacement of body feathers is aligned with prebasic replacement of flight feathers (Dittman and Cardiff 2009, Howell 2010, Sieburth and Pyle 2018, Pyle 2022a, 2022b). I infer that molt patterns in the Bee Hummingbird support aligning the second replacement of body feathers (including incoming gorget feathers of males) with the definitive prebasic molt of flight feathers, and that the first molt of body feathers (including replacement of iridescent with non-iridescent feathers in adult males) should be considered the definitive prealternate molt. Evidence for this interpretation includes the fact that the first molt of body feathers appeared to be only partial while the second molt of body feathers appeared to be complete (Sieburth and Pyle 2018), as well as the larger temporal gap between the first replacement and initiation of primary molt than that between the conclusion of primary molt and the second replacement of body feathers. This interpretation is also supported by homological comparison with other adult male hummingbirds of the bee clade that only replace gorget feathers once per year, following the molt of primaries (Pyle et al. 1997). Thus, I interpret the molt cycles of the Bee Hummingbird as including a preformative molt of body feathers in May–August, a complete second prebasic molt in December–April that concludes with development of gorget feathers in males in February–April, a definitive prealternate molt of some body feathers in July–September, and a complete definitive prebasic molt in October–January that concludes with development of gorget feathers in males in December–January. Molts occurred following a breeding season in March–July (Mugica Valdes et al. 2025) and span most of the non-breeding periods (July–February) as is the case in other hummingbirds (Pyle 2022a).

This simple alternate molting strategy (Howell et al. 2003, Pyle et al. 2024) accords with those proposed for North American species of Mellisugini in genera *Archilochus*, *Calypte*, and *Selasphorus* (Pyle 2022a), for tropical species of Mellisugini in genera *Chaetocercus*, *Calliphlox*, *Eulidia*, and *Thaumastura* (Clark et al. 2024), and apparently in genus *Sternoclyta* of the mountain-gem tribe Lampornithini (Sainz-Borgo et al. 2025). A simple alternate strategy, as defined here, appears to be the best interpretation based on evolution of molts along ancestral hummingbird and swift (Apodiformes) lineages (Sieburth and Pyle 2018).

The loss of the iridescence gorget in males results in less showy or more cryptic coloration during a vulnerable period, when flight is compromised by replacement of primaries, as has been documented in other species of birds (Echeverry-Galvis and Hau 2013). I thus hypothesize that a limited to partial prealternate molt may have evolved to provide crypsis for predation avoidance during flight-feather molt, a strategy that may similarly occur in male ducks with bright plumages (Pyle 2005) and for both sexes of ptarmigan (Pyle 2007, Hannon et al. 2025). Alternatively, social interactions are an important aspect of hummingbird behavior, males flaring and displaying their gorgets in both aggressive territorial interactions and for courtship (Stiles 1982, Hurly et al. 2001, Clark et al. 2024). Another hypothesis for the alternate plumage in the male Bee Hummingbirds could be to reduce the energy requirements for such interactions during times of molt when territorial disputes may be compromised by lessened flight agility. Further research on the predation rates and behavioral differences for hummingbirds with and without iridescent gorgets could help address these hypotheses.

Many birds undergoing prealternate molts are migratory (Pyle 2022a). One explanation for this could be pressure to replace worn feathers due to increased solar exposure on an annual basis, due to experiencing longer summer and winter day-lengths combined than for resident populations. This additional replacement along ancestral lineages may precede the development of brighter alternate color patterns in some current-day species (Pyle and Kayhart 2010, Terrill et al. 2020). That this strategy also appears to occur in resident tropical species of hummingbirds may underscore the adaptive value of more cryptic appearance during flight-feather molt. Similar prealternate molt and plumage strategies providing crypsis for flight-feather molt should be sought in other species of hummingbirds and birds.

The definitive prealternate molt in Bee Hummingbird differed from those of other hummingbird species in that the iridescent gorget feathers of males in this study were completely replaced, without exception, with non-iridescent white pennaceous feathers resembling those of females. Although Dittmann and Cardiff (2009) indicated that gorget feathers of male Ruby-throated Hummingbirds *Archilochus colubris* were replaced in late summer, prior to flight-feather molt, examination of Macaulay Library images indicates that at least most adult males of this species retain iridescent gorgets during flight-feather molt (e.g., ML401528801, ML422257741, ML297129601) as was also documented by Sieburth and Pyle (2018) for Rufous Hummingbird *Selasphorus rufus* (ML146543061, ML85526651). In the tropical species mentioned above, males appear to either partially replace their iridescent throat feathers or in some cases replace them with dusky tipped feathers at variance with the white throat feathers of females (Clark et al. 2024, Sainz-Borgo et al. 2025). Gorget feathers during flight-feather molt in all these cases appear old and worn, indicating retention of basic feathers rather than replacement of iridescent basic feathers with iridescent alternate feathers.

Iridescent feathers in hummingbirds are developed through a complex process of coherent light-scattering mechanisms involving light reflectance from nanostructures including flattened organelles containing air-filled melanosomes (D'Alba et al. 2021, Eliason et al. 2023). As with the complex nanostructural pigment development in non-iridescent feathers of birds (Prum et al. 2009), the mechanisms of color deposition to produce species-specific and feather-specific patterns are poorly understood. Similarly, temporal biochemical and hormonal cycles that dictate how feather color, pattern, and in some cases even structure can change between feathers produced during prebasic, prealternate, and presupplemental molts (cf. Pyle 2013, 2019) are also poorly understood. How the same follicles in adult male Bee Hummingbirds can produce complex iridescent feathers in December–January and radically simpler, non-iridescent feathers similar to those in females in July–September, as well as the physiological, cellular, and hormonal mechanisms resulting in these changes, is open for further investigation. That some female but no male Bee Hummingbirds appeared to develop alternate crown and throat feathers with iridescence, and that early but not late preformative molts may produce iridescent feathers in first-cycle males, adds further intrigue and possible explanatory leads to this inquiry.

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