

1 RHH: *P. Pyle* • Examination of images to study molt strategies

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3 **Examination of digital images from Macaulay Library to determine avian**
4 **molt strategies: A case study on molts and plumages in eight species of North**
5 **American hummingbirds.**

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10 **Abstract**—I examined a total of 27,581 images of 6,345 individuals from the Cornell Lab of
11 Ornithology's Macaulay Library to clarify conflicting reports on molt and plumage strategies in
12 eight species of hummingbirds that breed or have bred primarily in the southwestern United
13 States. Fixed replacement sequences from two nodes among primaries and two nodes among
14 secondaries were found without exception, conforming to the findings of previous studies. I
15 concluded that the preformative molt is limited to partial in three species, partial to incomplete in
16 three species, partial to complete in one species, and complete in one species. These molt
17 strategies could be interpreted as having differentiated through synapomorphy, with species
18 between currently recognized clades varying in the extent of their preformative molts; however,
19 given the plastic nature of molt strategies, I predict that this variation will be shaped more by
20 environmental factors than by synapomorphy. Results of this study additionally clarify molt
21 terminology in Trochilidae as based on homologies and establish new criteria for age
22 determinations. The Macaulay Library clearly provides an important resource for the
23 investigation of avian molts and plumages. The results of a validation exercise that I conducted

24 indicate that banders and field ornithologists with a wide range of previous experience can
25 collect accurate data in this manner. I present a road map for such studies and suggest many
26 other questions on avian molt that can also be investigated, including how timing of molts vary
27 geographically and by habitat and how remigial replacement sequences proceed in little-known
28 bird families. I encourage contributors to the Macaulay Library to take and upload images of
29 birds in molt or in worn plumages.

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31 **Key words**– molt sequence, molt terminology, preformative molt, synapomorphy, Trochilidae

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33 **Introduction**

34 Our understanding of avian molt strategies has lagged behind that of other aspects of avian
35 natural history (Bridge 2011, Marra et al. 2015), and this lack of knowledge is especially acute
36 among the large number of bird species found in equatorial regions (Craig 1983, Mulyani et al.
37 2017, Johnson and Wolfe 2018). Although study of specimens has been instrumental in
38 advancing our knowledge of avian molts, relatively few birds have been collected while
39 undergoing active molt (Rohwer et al. 2005), and large sample sizes are often needed to fully
40 document variation in timing, location, and extent of molts within a species' annual cycle and
41 throughout its geographic range.

42 Traditionally, hummingbirds in the United States and elsewhere were assumed to
43 undergo complete preformative and prebasic molts and to lack prealternate molts (Williamson
44 1956, Baltosser 1995, Pyle 1997, Howell 2002, Wolfe et al. 2009). However, the discovery of
45 definitive prealternate molts in Ruby-throated (*Archilochus colubris*) and Rufous (*Selasphorus*
46 *rufus*) hummingbirds has lead to other proposed terminologies (Dittmann and Cardiff 2009,
47 Howell 2010, Weidensaul et al. 2020), including a strategy that considers preformative molts in

48 these species to be partial (Sieburth and Pyle 2018). With the exception of the presence or
49 absence of prealternate molts, the strategies of the eight species in genera *Archilochus*, *Calypte*,
50 and *Selasphorus* that breed in the United States (hereafter "northern" hummingbirds) are
51 reasonably well documented (Williamson 1956, Baltosser 1995, Pyle 1997, Pyle et al. 1997,
52 Howell 2002, Williamson 2002). However, those of the eight species of genera *Eugenes*,
53 *Lamphornis*, *Calothrax*, *Cynanthus*, *Basilinna*, *Leucolia*, *Saucerottia*, and *Amazilia*, that breed or
54 have bred primarily in Texas and the southwestern United States (hereafter "southwestern"
55 species), are not as well known. Most of these species have ranges that extend to southern
56 Mexico or Central America, where geographic variation in seasonal regimes and life-history
57 requirements may complicate molt strategies.

58 Previous authors (e.g., Pyle 1997) attempted to confirm reports in the literature on
59 hummingbird molt by examining specimens and data from banding stations. For the eight
60 northern species generally there have been adequate sample sizes from these sources to
61 accurately assess molt strategies, including of specimens collected on winter grounds in Mexico
62 (Pyle et al. 1997, Sieburth and Pyle 2018). However, for the eight southwestern species, sample
63 sizes of specimens and captured birds have often been sufficiently lacking to gain a full
64 understanding of strategies. Currently there is conflicting information on timing and extents of
65 molts in these species as presented by Pyle (1997), Howell (2002), Williamson (2002), the Birds
66 of the World accounts (Billerman et al. 2020), and additional data collected from banding
67 stations in the United States and Mexico (Wethington 2020).

68 Beginning in the mid-2000s, the advancement of digital technology has allowed detailed
69 examination of feathers and feather tracts in images of birds, which in turn has been used to
70 study molts and plumages (Pyle 2008a, Viera et al. 2017, Panter 2021). Since this time, the
71 quantity of available on-line images has increased exponentially, expanding the potential to

72 augment data on bird molt collected from specimens. The Cornell Lab of Ornithology's
73 Macaulay Library archives audio and video recordings and images of birds and other wildlife for
74 scientific research, education, and conservation. Virtually all of the bird images archived at the
75 library were contributed as part of eBird, a citizen science project allowing both birders and
76 researchers to archive count data, images, and other media resulting from observations in the
77 field (Sullivan et al. 2009). eBird provides comprehensive search functions of the Macaulay
78 Library that allows viewing of digital images after applying various filters including location(s),
79 year(s) and month(s) of observation. Images can be ordered by date of observation, date
80 uploaded, or a quality rating from users. Currently there are over 20 million images of 10,056
81 bird species had been contributed to the library (M. Medler pers. comm.), typically representing
82 images from throughout a species' annual cycle, and providing a tremendous resource for the
83 study of avian plumages and molts.

84 I examined images archived at Macaulay Library to better document and clear up
85 inconsistent information on molts and plumages for the eight southwestern hummingbird species.
86 My goals included assessing the extent of the preformative molt (partial, incomplete, or
87 complete), establishing timing for all molts and plumages, evaluating replacement sequences
88 among flight feathers, and applying results to the accurate ageing and sexing of these eight
89 species and to our understanding of the evolution of molts, hence, molt terminology in these and
90 other hummingbirds (Humphrey and Parkes 1959, Howell et al. 2003, Sieburth and Pyle 2018). I
91 also undertook a validation study with banders and field ornithologists to test the applicability of
92 this methodology. My primary goal is to provide a case study for using the Macaulay Library to
93 study avian molts around the world.

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Methods

97 Species examined for this analysis were Rivoli's Hummingbird (*Eugenes fulgens*), Blue-throated
98 Mountain-gem (*Lamphornis clemenciae*), and Lucifer (*Calothrax lucifer*), Broad-billed
99 (*Cynanthus latirostris*), White-eared (*Basilinna leucotis*), Violet-crowned (*Leucolia violiceps*),
100 Berylline (*Saucerottia beryllina*), and Buff-bellied (*Amazilia yucatanensis*) hummingbirds. I
101 sought to assess molt patterns within populations of these species that breed or occur north of
102 Mexico. Therefore, I set eBird's location filter of Macaulay Library images to the United States.
103 For each species I used the month filter to examine images for each month of the year. For
104 Lucifer, White-eared, and Berylline hummingbirds, I concluded that sample sizes of images from
105 the United States year-round were insufficient to gain an accurate assessment of molt patterns. I
106 therefore set the filter to Mexico and augmented the sample by examining images taken in the
107 northern tier of Mexican states and those on the Mexican Plateau south to the Distrito Federal,
108 with the assumption that these bioregions included wintering individuals from the United States
109 or breeding populations that exhibited similar molt strategies. Within each month I ordered the
110 images by date, from oldest to newest. This allowed better tracking of individual hummingbirds,
111 for example, those at popular feeding stations, thereby minimizing duplication of data from the
112 same individuals.

113 All images at Macaulay Library of these eight species taken in the United States and
114 uploaded through July 2020 were reviewed. Hummingbirds misidentified to species (< 1%) were
115 excluded. Data were recorded only from images that could be properly assessed for both
116 plumage (age) and molt status; e.g., all primaries of the wing were visible or accounted for in
117 molt (Figure 1). In many cases the eBird Checklist contained multiple images of the same
118 individual, which helped with accurate determinations. Individuals that were not confidently
119 aged were excluded. I also excluded images of the same individual within a month as

120 conservatively as possible based on molt and plumage status, date, location, eBird checklist data,
121 age, appearance, and bill pattern. Generally, a bird of similar molt status, plumage, and
122 appearance within 7 d of a previous observation at the same location was assumed to be the same
123 individual. Individuals with images that spanned months were recorded for each month of
124 occurrence.

125 For each individual I determined plumage and molt status. Plumages in both males and
126 females were identified following the ageing criteria of Pyle (1997), Howell (2002), and
127 Williamson (2002), along with new criteria presented here (Supplemental Figures S1-S9).
128 Criteria based on wing feathers, rectrices, and for some species bill color were emphasized; that
129 of iridescent feathering in males was evaluated with caution due to effects of lighting on the
130 perceived coloration of these feathers in digital images. Extent of corrugation at the base of the
131 culmen (Ortiz-Crespo 1972, Yanega et al. 1997, Pyle 1997) was also examined but could only be
132 evaluated on a small proportion of images. For individuals in active molt, replacement sequence
133 of primaries, secondaries, and rectrices was assessed (Figure 1). Primaries were numbered
134 proximally from p1 (inner) to p10 (outer) and secondaries distally, from s1 (outer) to s6 (inner).
135 Comparison of primary and secondary spacing (morphology) in images of birds not in active
136 molt was employed to help determine precise sequences in molting birds, and symmetry among
137 new, molting, and old feathers within both wings was confirmed, when possible, to ensure that
138 missing feathers reflected molt. Arrested or suspended molts among flight feathers (cf. Pyle et al.
139 1997) were noted as contrastingly new feathers in sequence among older unreplaced feathers.
140 Molt and molt limits among body feathers and upperwing secondary coverts were also assessed
141 by evaluating pin and growing feathers along with contrasts between new and old feather
142 generations. See the Supplemental Materials File for more detail on this methodology.

143 I categorized each individual into one of six plumage or molt states: 1) juvenile plumage
144 (prior to evidence of preformative molt), 2) undergoing preformative molt, 3) formative plumage
145 of body or flight feathers, 4) undergoing second prebasic molt of flight feathers, 5) definitive
146 basic plumage, and 6) undergoing definitive prebasic molt of flight feathers. Partial preformative
147 molts (excluding primaries) are often protracted and/or suspended resulting in less-precise
148 assignment of preformative molt or formative plumage. To categorize these I looked for pin and
149 growing feathers and also assessed when development of definitive-like appearance appeared to
150 culminate within the entire sample of first-cycle males, including long-staying individuals
151 undergoing and completing preformative molt. Timing of molts and plumages in hummingbirds,
152 except for gorget-feather replacement in males, shows little variation by sex (Williamson 1956,
153 Pyle et al. 1997, Sieburth and Pyle 2018), and this also accorded with exploratory examination of
154 Macaulay Library data for this study. Therefore, counts included both sexes combined. Images of
155 interest are referenced by their Macaulay Library identifiers ("ML" followed by 8 or 9 numerals)
156 and in some cases eBird Checklist identifiers ("S" followed by 7 or 8 numerals) when multiple
157 images of the same bird documented the point of reference.

158 Examination of images to study avian molt may require extensive previous experience
159 with captured birds or specimens. To test whether or not banders and field ornithologists with a
160 varying range of previous field experience can collect accurate data on molt from images, I
161 circulated a validation study which included images of 11 hummingbirds from the Macaulay
162 Library (see Supplemental Materials File). Each participant was asked to evaluate their previous
163 experience with banding and field ornithology, to determine the age of the individual, to score
164 the status of molt (active or inactive), to score the condition of each of the 10 primaries (new,
165 growing, missing, or old), and to record the number of minutes it took to age and score each

166 individual. Participants were given Supplemental Figures 1-8 as a study guide before
167 undertaking the exercise.

168

169 **Results**

170 A total of 27,581 images from the Macaulay Library of the eight southwestern hummingbirds
171 was examined for this study (Supplemental Table S1). These included 6,345 individuals from
172 images that were of sufficient quality to assess plumage (age) and molt status. Total individuals
173 by species ranged from 280 White-eared Hummingbirds to 2,413 Broad-billed Hummingbirds,
174 totals by month ranged from 248 individuals for February to 1,245 for August, and totals by
175 species in a month ranged from 4 Lucifer Hummingbirds in February to 639 Broad-billed
176 Hummingbirds in July (Supplemental Table S1). Samples of > 25 individuals were recorded for
177 75% of the months by species.

178 Sequence of feather replacement among primaries consistently proceeded from a node at
179 p1 distally and a node at p10 proximally, with p9 being the last primary replaced (Figure 1).
180 Among images of 1,373 individuals recorded undergoing active primary molt, no exceptions to
181 this sequence were observed (cf. Supplemental Figures S1-S8), including among >10 known
182 individuals that could be tracked for all or large portions of the molting period. The six
183 secondaries of these species began to be replaced when p6 had dropped (e.g., [ML 181183661](#),
184 [ML46645931](#), [ML122879681](#)). Among 71 individuals in which active secondary molt could be
185 evaluated, replacement invariably proceeded proximally from a node at the innermost feather s6
186 and distally from a node at the outermost feather s1 (Figure 1). The orders in which s1 and s6
187 and s3 and s5 were molted were variable, but s4 was always the last feather to be replaced, near
188 to or following completion of primary molt (e.g., [ML 195887161](#), [ML34535671](#), [ML100323371](#),
189 [ML 33989911](#)). Sequence of rectrix replacement was more difficult to evaluate in images but

190 typically began with the central rectrices when p7 or p8 were dropped (e.g., [ML184013981](#), [ML](#)
191 [188765281](#), [ML34654481](#)), after which replacement of remaining rectrices generally proceeded
192 rapidly and distally (e.g., [ML238319331](#), [S56405130](#)), with the outermost (r5) often replaced
193 before r4 and/or r3 (e.g., [ML238400031](#)).

194 Suspended or arrested molts among non-molting remiges were rare, being recorded in
195 only 23 individuals (< 0.01% of 3,652 non-molting hummingbirds), of six species, Rivoli's
196 Hummingbird, Blue-throated Mountain-gem, and Broad-billed, White-eared, Violet-crowned,
197 and Buff-bellied hummingbirds. These were recorded during both preformative molts (see
198 below) and definitive prebasic molts (e.g., [ML45716111](#), [ML212853441](#), [ML 86250771](#),
199 [ML51351041](#), [S41676864](#)), including individuals that had replaced all remiges except for the s4
200 (e.g., [ML48860261](#), [ML42333141](#), [S2611244](#)). Suspended or arrested molts were recorded at a
201 single location within the above sequences, with the exception of one Buff-bellied Hummingbird
202 that had suspended molt after replacing p1 and p6 most recently ([ML 22821451](#)), perhaps
203 following an earlier arrested molt. No retained rectrices resulting from suspended or arrested
204 molts were noted but these could easily have been missed.

205 Sample sizes for the six molt and plumage categories, by month, for the eight species are
206 given in Supplemental Table S1. Dates for juveniles ranged from 2 February in Buff-bellied
207 Hummingbird to 18 November in Berylline Hummingbird, and temporal duration periods for
208 recorded juveniles ranged from 78 d in Violet-crowned Hummingbird to 184 d in Rivoli's
209 Hummingbird (Supplemental Table S2). The preformative molt was first detected from nine (in
210 Berylline Hummingbird) to 80 (in White-eared Hummingbird) days following the earliest
211 juveniles recorded in the spring. Temporal periods for the preformative molt among populations
212 ranged from about 5 mo in White-eared Hummingbird, Lucifer Hummingbird, and Berylline
213 Hummingbird, to about 7 mo in Blue-throated Mountain-gem and Violet-crowned

214 Hummingbird, about 8 mo in Broad-billed Hummingbird, 9.4 mo in Rivoli's Hummingbird (282
215 d), to 10.3 mo in Buff-bellied Hummingbird (Figure 2, Supplemental Table S2).

216 I concluded that the preformative molt is typically limited to partial in three species,
217 Lucifer, Berylline, and Buff-bellied hummingbirds (Figure 3 and Supplemental Figures S3, S7,
218 and S8). These species replace variable amounts of body feathers and upperwing secondary
219 coverts, from a few body feathers only to most or all body feathers and secondary coverts, but
220 replaced no primaries, primary coverts, secondaries, or rectrices until commencement of the
221 second prebasic molt. Most Rivoli's Hummingbirds, Blue-throated Mountain-gems, and Violet-
222 crowned Hummingbirds also undergo partial preformative molts (Figures 1 and Supplemental
223 Figures S1, S2, and S6), although small proportions, one of 126 first-cycle Rivoli's
224 Hummingbirds in October-August (0.8%), one of 95 first-cycle Blue-throated Mountain-gems in
225 November-August (1.1%), and three of 140 first-cycle Violet-crowned Hummingbird in August-
226 May (2.1%) were replacing or had replaced two to six inner primaries during what I judged to be
227 incomplete preformative molts (Figure 4).

228 For Broad-billed Hummingbird, the preformative molt varied from partial to complete
229 (Figures 2 and 3 and Supplemental Figures S4). Active molting of primaries and rectrices during
230 the preformative molt of this species ($n = 29$) was recorded from 3 August ([ML86966331](#)) to 25
231 January ([S33932855](#)) with active molting of secondaries recorded through 16 February
232 ([ML208941611](#)). In November-December, 56% of 32 first-cycle birds were molting or had
233 molted primaries, and in December-May at least 10 of 222 first-cycle individuals (4.5%) had
234 suspended or arrested primary molt, most often at p2 (e.g., [ML77579011](#)) or p4 (Figure 4; see
235 also, e.g., [ML47852161](#), [ML22932271](#)). Some males underwent a complete preformative molt of
236 flight feathers but did not acquire definitive appearance of body plumage whereas others
237 acquired complete or near-complete definitive appearance in body feathering but retained

238 juvenile flight feathers (Figure 2 and Supplemental Figures S4 and S9). Some Broad-billed
239 Hummingbirds following complete molts likely become indistinguishable from individuals in
240 definitive basic plumage, and were categorized as in definitive basic plumage here.

241 For White-eared Hummingbird I concluded that the preformative molt was complete. It
242 was the only one of the eight species in which timing of preformative and later molts was
243 similar, the replacement of primaries commencing at the same time or before juvenile body
244 feathers began molting (Supplemental Figure S5; [ML252080431](#), [S11291169](#)) and completing
245 following body-feather replacement, at which time males had acquired definitive-like appearance
246 (Figures 1 and 2 and Supplemental Figure S5). It was also the only species in which no males
247 following the preformative molt showed predefinitive appearance ($n = 64$). The longer period for
248 juveniles recorded for this species (80 d) than the others (10-57 d) may also relate to the
249 complete molt, juvenile feathers not needing to last for five months or more. As a result of this
250 complete preformative molt, White-eared Hummingbirds in formative vs. definitive basic
251 plumage and undergoing the second vs. definitive prebasic molts could not be distinguished in
252 images for this study, with the exception of some in formative plumage with dull red bill colors.

253 Formative plumage in males (and in some cases females) of these seven species, as aged
254 by flight-feather characteristics, generally did not reach definitive appearance of body feathering,
255 varying from showing no or a few iridescent display feathers in male Lucifer Hummingbirds to
256 showing nearly full to full definitive appearance in male Broad-billed, Berylline, and Buff-
257 bellied hummingbirds (Figure 2 and Supplemental Figures S1-S4, S6-S9). Formative plumages
258 in male Rivoli's Hummingbird and Blue-throated Mountain-gem, and in both sexes of Violet-
259 crowned and Buff-bellied hummingbirds, were variable and intermediate but few birds in
260 formative plumage appeared to have acquired definitive appearance of body feathering
261 (Supplemental Figures S1, S2, S6, and S9). By contrast, definitive basic males of all eight

262 species (as aged by flight-feather characteristics) showed full definitive appearance, with the
263 exception of a small proportion of Rivoli's Hummingbirds that had small and variable amounts
264 of brown feathering in the lower breast; further study is needed on whether or not this may
265 represent second basic plumage.

266 Within the populations, the temporal duration period for the second prebasic molt ranged
267 from 63 d in Blue-throated Mountain-gem and 65 d in Violet-crowned Hummingbird to 188 days
268 in Buff-bellied Hummingbird, and for the definitive prebasic molt duration ranged from 94 d in
269 Blue-throated Mountain-gem to 271 d in Buff-bellied Hummingbird (Supplemental Table S2).
270 With the exception of Buff-bellied Hummingbird the seasonal timing for these molts was well
271 defined (Figure 2 and Supplemental Table S2). Known individual hummingbirds take less time
272 within these periods to molt; e.g., a Berylline Hummingbird in Arizona in 2020 was documented
273 completing a definitive prebasic molt in 49 d, from dropping p1-p3 of 26 April ([S67876574](#)) to
274 completing growth of p9 and s4 on 14 June ([ML244918451](#)), and a Buff-bellied Hummingbird in
275 Florida that had dropped inner primaries on 4 November 2016 ([ML39279451](#)) was completing
276 molt 69 d later on 28 January 2017 ([ML46926141](#)). Timing of the second prebasic molt differed
277 but overlapped that of the definitive prebasic molt in all seven species, the overlap being earlier
278 than the definitive prebasic molt in Rivoli's Hummingbird, Blue-throated Mountain-gem, Broad-
279 billed Hummingbird, and Violet-crowned Hummingbird, and later than the definitive prebasic
280 molt in Lucifer, Berylline, and Buff-bellied hummingbirds (Figure 2). Based on my conclusions
281 on the evolution of these molts, however, the second prebasic molt occurred earlier in timing
282 than the definitive prebasic molt in all seven species (see Discussion).

283 Seventeen field biologists (including the author) participated in a validation exercise to
284 ensure that this methodology can be used to collect accurate data on molt (Supplemental
285 Materials File). Participants correctly aged the 11 hummingbirds (first-year or older) 83% of the

286 time, reached a correct conclusion on molt status (active or inactive) 93% of the time, and
287 provided correct answers for the condition of each primary (new, missing, growing, or old) from
288 83% to 91% of the time. For individual primary cells, correct answers ranged from 6% and 18%,
289 up to 100% for most, with a mean of 87.2%. The mean time it took to age and score each
290 hummingbird was 3.7 minutes. The mean proportion of correct answers for the 132 cells was
291 87.5%, ranging from 80.3% to 95.4% among the 17 observers. Among participants with low,
292 medium, and high experience levels, correct answers were provided for 83.1%, 87.1%, and
293 88.9% regarding banding experience and 87.6%, 86.6%, and 88.9% regarding field experience,
294 respectively.

295

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Discussion

297 Sequence of primary molt in hummingbirds has previously been reported to be distal from a
298 node at p1, proximal from a node at p10, and with p9 the last feather replaced (Wagner 1955,
299 Williamson 1956, Stiles 1995, Pyle 1997, Howell 2002). This sequence was confirmed with few
300 or no exceptions among 1,373 molting hummingbirds of all eight species in this study. Results of
301 this study also indicate replacement nodes among secondaries to be fixed, with proximal
302 replacement from s1 and distal replacement from s6 resulting in s4 being the last secondary
303 replaced, without exception within my sample, including for Lucifer Hummingbirds (e.g.,
304 [ML79210961](#)), contradicting reports by Wagner (1955) of replacement from nodes in the center
305 of the tract (see also Stiles 1995). These remegial replacement nodes and directions are
306 consistent with those found by Williamson (1956) for Anna's Hummingbird (*Calypte anna*) and
307 by Stiles (1995) for 13 hummingbird species in Costa Rica, although Stiles also found that the
308 last secondary replaced was s3 or s5 rather than s4 in a small proportion (6.2%) of 242
309 individuals in his study. It is possible that variable sequences may follow arrested molts, which

310 appear to be more common in species of tropical rather than in temperate habitats (Pyle et al.
311 2016), perhaps including Buff-bellied Hummingbird in this study.

312 Unlike timing, location, and extent of molts, sequential replacement of remiges in birds
313 appears very fixed (cf. Pyle 2013), in which case I predict that these four remigial nodes and
314 replacement directions will be found in all hummingbird species. Precise sequence among
315 different replacement waves (e.g., in hummingbirds, initiation at either s1 or s6 or order of s3 vs.
316 s5) and terminal feathers where waves converge is less fixed, evolutionarily, and may vary in
317 birds according to wing physiology, flight requirements, or other parameters. My results on
318 rectrix sequence also comport with those of Stiles (1995). The p9 is the longest primary in
319 hummingbirds and it has been proposed that its replacement follows that of p10 to maintain wing
320 integrity in a bird family that relies heavily on flight for existence (Greenewalt 1975, Stiles
321 1995). A similar sequence among primaries in family Ardeidae (Shugart and Rohwer 1996, Pyle
322 2008b) has evolved independently, perhaps for different reasons.

323 Additional results of this study otherwise clarify molt strategies in these eight
324 southwestern hummingbirds to a substantial degree. For example, preformative molts in seven
325 species are here interpreted to be partial in most individuals, differing from previous
326 interpretations that they were complete (Pyle 1997, Howell 2002). In three of these species,
327 Rivoli's Hummingbird, Blue-throated Mountain-gem, and Broad-billed Hummingbird, juvenile
328 primaries can be retained for close to a year, consistent with strategies in most other birds with
329 partial preformative molts (Howell et al. 2003; Pyle 1997, 2008b, Jenni and Winkler 2020).
330 Lucifer, Berylline, and Buff-bellied hummingbirds have molts more similar to northern North
331 American species, in which body feathers are partially replaced during a preformative molt well
332 before primaries are replaced as part of the second prebasic molt (see below). The timing of the
333 second prebasic molt of Violet-crowned Hummingbird appears to be intermediate between these

334 two groups and indicates that they may not breed in their first spring, although its apparently
335 short duration may allow them to breed later in summer, following the molt. The extent of
336 preformative molt in four species, Rivoli's Hummingbird, Blue-throated Mountain-gem, Broad-
337 billed Hummingbird, and Violet-crowned Hummingbird can at least occasionally include
338 primaries and in White-eared Hummingbird it is complete. Variation in preformative molt extent,
339 from partial to incomplete to complete, has also been documented within other bird species and
340 genera, such as those among Scolopacidae, Tyrannidae, Fringillidae, Passerellidae, and
341 Cardinalidae (Pyle 1997, 2008b), and perhaps is correlated with habitat use and extent of solar
342 exposure on an annual basis (Pyle 1998, 2008b, Guallar et al. 2020). White-eared Hummingbird
343 is the smallest of the eight species treated here (Billerman 2020), and this could also be a factor
344 in its undergoing a complete preformative molt, as extent of partial or incomplete molts in birds
345 generally increases with decreasing body size (Kiat and Izhaki 2016).

346 Results of this study also help clarify previous discrepancies on timing of complete molts
347 in these eight southwestern hummingbird species. For example, in Broad-billed Hummingbird,
348 Pyle (1997) reported that populations in the United States underwent the first molt of primaries
349 in November-May and definitive prebasic molts in October-April; Howell (2002) concluded that
350 the definitive prebasic molt commenced in April-September and completed in July-January, with
351 first molt of primaries averaging later in timing; and Williamson (2002) indicated that the
352 definitive prebasic molt occurred in May-September and the first molt of primaries occurred in
353 July-November of the same year. Results of this study, by contrast, indicate that some birds first
354 replace primaries during the preformative molt in August-January, others replace them at the
355 second prebasic molt in May-September of the following year, and the definitive prebasic molt is
356 confined to June-October. Based primarily on banding studies the suggestions on molt timing in
357 Broad-billed Hummingbird reported by Powers and Wethington (2020) are more consistent with

358 the results of this study, though substantial clarification of preformative, second prebasic, and
359 definitive prebasic molt strategies is provided here. Similar discrepancies between results
360 reported here and those of these previous sources are found in the other seven species. Also
361 contrasting with previous reports, I found that suspended or arrested molts to be rare in these
362 eight species of hummingbirds (< 0.1%) , and I also provide new criteria for age determination
363 and its timing, including those related to development of definitive appearance in first-cycle
364 males, molt limits among wing coverts, and molt clines among the remiges (Supplemental
365 Figures S1-S9). No evidence was found for an identifiable second basic plumage in male Lucifer
366 Hummingbirds and little evidence for this in Rivoli's Hummingbird, contra Pyle (1997).

367

368 **Evolution of molt strategies in hummingbirds**

369 I found no evidence for prealternate molts in these eight species of hummingbirds, although such
370 evidence would be better gained from banding studies; prealternate molts may not be as expected
371 in less-migratory or resident hummingbirds (Johnson and Wolfe 2018). Irrespective of this, I
372 believe that the preformative and prebasic molt strategies documented here support the
373 interpretation of Sieburth and Pyle (2018) that the second prebasic molt has been temporally
374 advanced in northern hummingbirds of the United States, as opposed to traditional
375 interpretations that the first complete molt of North American hummingbirds is invariably the
376 preformative molt. In Rivoli's Hummingbird and Blue-throated Mountain-gem, a partial
377 preformative molt and a complete second prebasic molt averaging earlier in timing than
378 definitive prebasic molts, at about a year of age, is consistent with molt strategies in many other
379 birds, as are complete preformative and prebasic molts during the same temporal period in
380 White-eared Hummingbird. The second prebasic molt in these species peak in August (Figure 2),
381 whereas this molt is here interpreted as peaking progressively earlier in Broad-billed

382 Hummingbird (June), Violet-crowned Hummingbird (May), Berylline Hummingbird (March),
383 Buff-bellied Hummingbird (February), and Lucifer Hummingbird (January), in the last species
384 similar to the timing for the first primary molt in the eight northern species.

385 Like the northern species (Sieburth and Pyle 2018), Lucifer Hummingbird is highly
386 migratory and undergoes a partial preformative molt of feathers (e.g., those of the gorget in
387 males), that get replaced again during the first molt of primaries in winter and early spring. In
388 order to best preserve homology under the traditional interpretation, the partial-to-incomplete
389 molt of first-cycle Rivoli's Hummingbirds, Blue-throated Mountain-gems, and Violet-crowned
390 Hummingbirds, and the partial-to-complete molt of first-cycle Broad-billed Hummingbirds,
391 would also be considered auxiliary preformative molts, which would be novel interpretations for
392 these molts. Rather, I conclude it more parsimonious to interpret the partial-to-complete first-
393 cycle molts that occur primarily in May-December to be preformative molts, as in many other
394 bird species, and that the complete second prebasic molt has evolved along hummingbird
395 lineages to become variably advanced in timing, from August in Rivoli's Hummingbird and
396 Blue-throated Mountain-gem, to May in Violet-crowned Hummingbird, to January in Lucifer
397 Hummingbird and the other migratory northern species, perhaps in response to the shorter life
398 span of hummingbirds relative to other birds (Sieburth and Pyle 2018).

399 The eight species of hummingbirds studied here are found in three clades as defined by
400 McGuire et al. (2014), the bee clade (Lucifer Hummingbird), mountain-gem clade (Rivoli's
401 Hummingbird and Blue-throated Mountain-gem), and emerald clade (remaining five species),
402 with the emeralds being split into four groups as defined by Stiles et al. (2017), including group
403 A (Broad-billed Hummingbird), group B (White-eared Hummingbird), and group D (Violet-
404 crowned, Berylline, and Buff-bellied hummingbirds). Molt strategies in these eight species could
405 be interpreted as having differentiated through synapomorphy during the evolution of these

406 clades and groups, with the bee clade (including the eight northern North American species)
407 sharing more limited preformative molts and second prebasic molts at 6-8 months of age, the
408 mountain-gem clade sharing partial preformative molts and second prebasic molts at about a year
409 of age, and the emerald clade sharing molt strategies that differentiate according to group, with
410 variable preformative molts and second prebasic molts at a year of age (group A), complete
411 preformative molts (group B), or protracted and partial preformative molts followed by second
412 prebasic molts that occur at 7-10 months of age (group D). Partial preformative molts in the
413 more-primitive topaz, hermit, and patagona clades (Zimmer 1950, Hu et al. 2000, Pyle et al.
414 2015, Johnson and Wolfe 2018) could represent the ancestral state (Sieburth and Pyle 2018).

415 Within the emerald clade, however, Johnson and Wolfe (2018) indicate that at least one
416 species in group B (genus *Campylopterus*) may have a partial preformative molt and at least
417 three species in group D (now in genera *Chrysuronia*, *Chionomesa*, and *Hylocharis*) may have
418 complete preformative molts, contrasting with the above-proposed shared molt-strategy
419 partitioning for the species in this study. Molt strategies on many more species of hummingbirds
420 will need to be documented to further test how they have evolved along ancestral Trochilid
421 lineages. Given the plastic nature of molt strategies found by these and other studies on avian
422 molt to date, within genera and even within species (Johnson 1985, Voelker and Rohwer 1998,
423 Rohwer and Irving 2011, Rohwer et al. 2011), I predict that variation in the extent and timing of
424 preformative molts and the timing of prebasic molts in hummingbirds will be shaped more by
425 environmental factors than by synapomorphy.

426

427 **Analysis of digital images to study bird molt**

428 As shown by the results of this study, the Macaulay Library and eBird checklists clearly provide
429 an important resource for the investigation of avian molts and plumages, particularly with respect

430 to sequence of remigial replacement, the extent of partial and incomplete molts, the timing of
431 complete molts, and plumage-related criteria for age determination. Certain aspects of molt
432 strategies will still need to be assessed through specimens, in which, for example, age and
433 reproductive status can be confirmed with extent of bill corrugations and information about
434 gonads and other conditions recorded on specimen labels. Data from banding studies,
435 furthermore, can add information on known individuals through recaptures, and I predict that
436 exceptions to some of the information presented here will be found during these studies.

437 Analyses of individual feathers for stable isotopes and connectivity between summer and winter
438 grounds can be undertaken with specimens and captured birds but not with images. Additional
439 drawbacks to scoring molt from images include the quality of some images, making it difficult or
440 impossible to determine precise remegial numbering, the inability to assess both wings to
441 confirm symmetrical molt for many individuals, difficulty in assessing low levels of body-
442 feather molt, and in the case of hummingbirds, the effects that lighting can have on iridescent
443 display feathers as presented in single-plane images. However, these concerns are mitigated by
444 the substantial sample sizes of available images, resulting in adequate data despite the usability
445 of only small proportions of these samples, and, in many cases, the ability to assess multiple
446 images of the same individual in one or more eBird checklists.

447 Both specimen examination and banding studies take time and effort, as opposed to
448 examination of on-line images, during which large samples can be gathered and analyzed in a
449 short amount of time and with little expense, data are collected without having to be concerned
450 about damaging specimens or the health of a captive bird, and voucher photographs are
451 automatically part of the methodology and can be preserved for later examination or studies on
452 repeatability of results. As shown by the validation study reported on here, banders and field
453 ornithologists of varying experience levels can collect accurate data from images, with precision

454 of data appearing to increase with experience levels of banding and (less so) field experience. I
455 also predict that similar validation studies performed with specimens and banded birds would
456 yield similar levels of accuracy.

457 I encourage additional research on avian molt through examination of digital images. Here
458 I provide a road map for a subset of such studies; however, many other questions on molt can
459 also be investigated using the Macaulay Library collection. For example, how might timing of
460 molt in these eight species of hummingbirds vary with respect to breeding and wintering
461 locations or in subtropical and tropical breeding subspecies or populations (cf. Wagner 1957,
462 Guallar and Gallés 2017)? How much molt-breeding overlap may occur for birds photographed
463 repeatedly at known nesting sites (e.g., [\(ML174305101\)](#))? How might remigial replacement
464 sequence vary in little-known bird families, and can this be applied to the evolution of molt
465 sequence and of birds? Data from the Macaulay Library image collection can also supplement
466 other data sets to help answer questions related to molt intensity and duration (Rohwer et al.
467 2009) and to the evolution of preformative molts and formative plumages through phylogenetic
468 comparative or ancestral state reconstruction analysis (cf. Kiat et al. 2019), as have recently been
469 performed based on specimens in other New World bird families such as Cardinalidae (Guallar
470 et al. 2020) and Parulidae (Terrill et al. 2020). To best further such research, finally, I encourage
471 those contributing images to eBird to include birds in molt or in worn plumages, even if they
472 may not be as appealing as, for example, adult males in definitive plumage, of which >50% of
473 hummingbird images I examined referred.

474

475 **Acknowledgments**

476 Foremost I thank the thousands of citizen scientists who have contributed images to the
477 Macaulay Library and for agreeing to the license allowing use for research purposes. A total of
478 174 contributors provided images that are shown or linked in this study. See Figures 2-3,

479 Supplemental Table S2, and Supplemental Figures S1-S9 for contributors to those media. Photos
480 linked in the primary manuscript and for the validation exercise, used by license agreement from
481 the Macaulay Library, were contributed by © Ryan Andrews, Eric Barnes, Cathy Beck, James
482 W. Beck, David Bernstein, Robert Bowling, Paul Budde, Cesar Castillo, Fred Collins, Ed Corey,
483 Joshua Covill, Holly Cox, Jon Curd, Tom Driscoll, Merryl Edelstein, Laura Ellis, Richard Fray,
484 Tony Godfrey, Bradley Hacker, Brien Harvey, John Haynes, Bill Hubick, Scott Jennex, Eric
485 Kallen, Ad Konings, Scott Lewis, Anuar López, Suzie McCann, Michael McCloy, Ken Murphy,
486 Marky Mutchler, Grace Oliver, Arlene Ripley, Dan Scheiman, Mel Senac, John Sterling, James
487 Stull, John Sullivan, Brandon Trentler, Mary Rachel Tucker, Jason Vassallo, Dan Vickers, Nigel
488 Voaden, Rob Worona, Bill Ypsilantis, and Bob Zaremba; see the Supplemental Materials File for
489 additional contributors. I thank Matthew Medler and Brooke Kelley Keeney of the Cornell Lab
490 for help ensuring that information about the Macaulay Library and contributors through eBird
491 were accurately and properly credited, and Blaine Carnes, Jerry Cole, Kenneth Foster, Marcel
492 Gahbauer, Christine Godwin, Santiago Guallar, Marc Illa, Erik Johnson, Danielle Kaschube,
493 Brooke Kelley Keeney, Pricilla Lai, Shannon M. Mendia, Jim Saracco, Dessi Sieburth, Al
494 Sherkow, Natália Pérez Ruiz, Ron Taylor, and Keegan Tranquillo for participating in the
495 validation exercise. Blaine Carnes and Santiago Guallar have read a draft of the manuscript and
496 provided constructive criticism. This is contribution # 678 of The Institute for Bird Populations.

497 **Literature Cited**

498 Baltosser WH. 1995. Annual molt in the Ruby-throated and Black-chinned hummingbirds. The
499 *Condor* 97:484-491.

500 Billerman SM, Keeney BK, Rodewald PG, Schulenberg TS, editors. 2020. *Birds of the World*.
501 Ithaca (NY): Cornell Laboratory of Ornithology. <https://birdsoftheworld.org/bow/home>

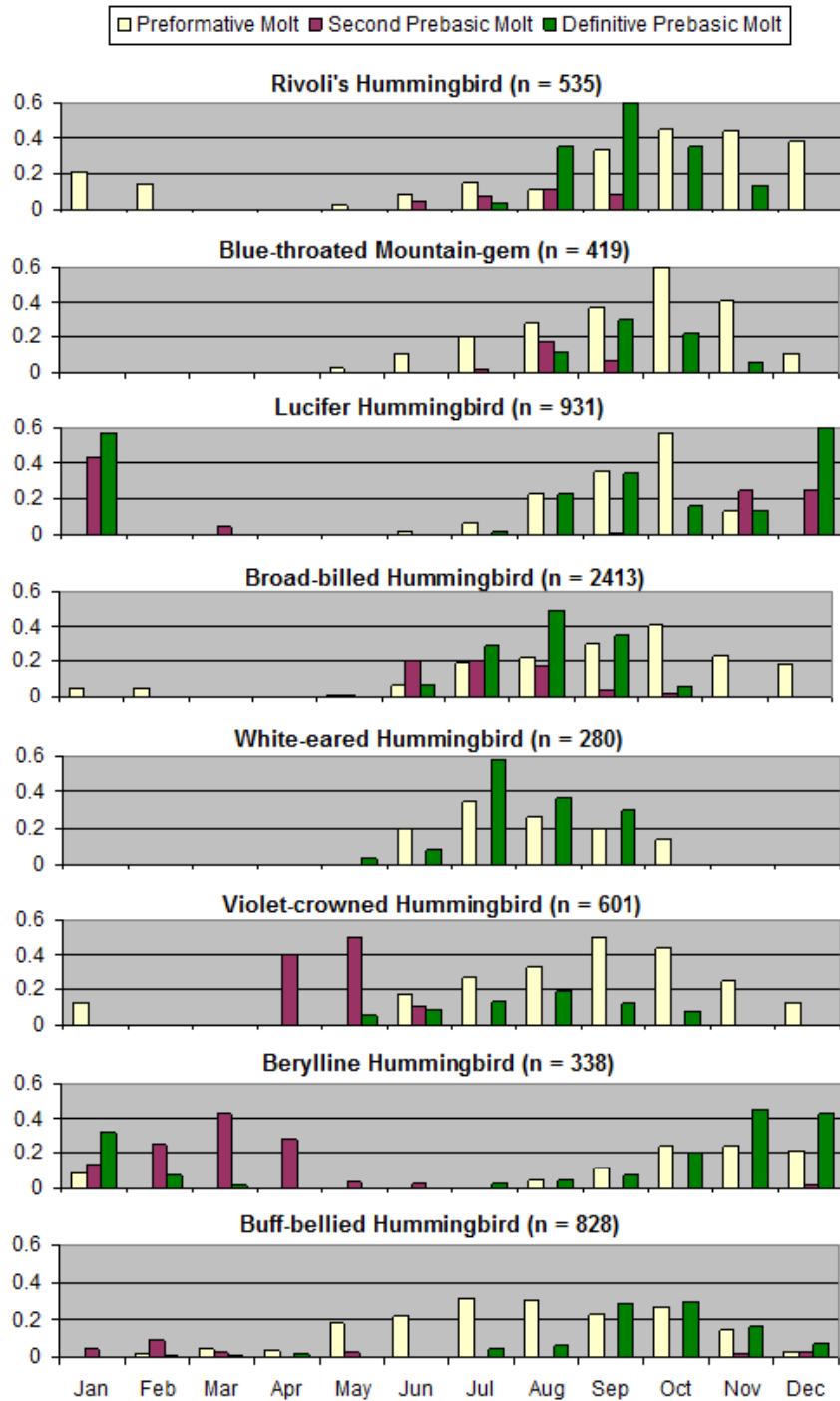
- 502 Bridge E. 2011. Mind the gaps: What's missing in our understanding of feather molt. *The Condor*
503 113:1–4.
- 504 Craig AJFK. 1983. Molt in southern African passerine birds: A review. *Ostrich* 54:220–237.
- 505 Dittmann DL, Cardiff, SW. 2009. The alternate plumage of the Ruby-throated Hummingbird.
506 *Birding* 41:32–35.
- 507 Greenewalt CH. 1975. The flight of birds. *Transactions of the American Philosophical Society*
508 65:1–67.
- 509 Guallar S, Gallés A. 2017. Age determination of Amethyst-throated Hummingbird (*Lampornis*
510 *amethystinus*) and White-eared Hummingbird (*Hylocharis leucotis*). *Ornitología*
511 *Neotropical* 28:129–133.
- 512 Guallar SX, Rueda-Hernández R, Pyle P. 2020. Evolution of the preformative molt in
513 *Cardinalidae* correlates with transitions from forest to open habitats. *The Auk:*
514 *Ornithological Advances*: In press.
- 515 Howell SNG. 2002. *Hummingbirds of North America: The photographic guide*. San Diego (CA):
516 Academic Press Natural World.
- 517 Howell SNG. 2010. *Molt in North American birds*. New York (NY): Houghton Mifflin Harcourt.
- 518 Howell SNG, Corben C, Pyle P, and Rogers DI. 2003. The first basic problem: A review of molt
519 and plumage homologies. *The Condor* 105:635–653.
- 520 Hu D-S, Joseph L, Agro D. 2000. Distribution, variation, and taxonomy of *Topaza*
521 hummingbirds (Aves: Trochilidae). *Ornitología Neotropical* 11:123–142.
- 522 Humphrey PS, Parkes KC. 1959. An approach to the study of molts and plumages. *The Auk*
523 76:1–31.
- 524 Jenni L, Winkler R. 2020. *Molt and ageing of European passerines*, second edition. London
525 (UK): Helm.

- 526 Johnson EI, Wolfe JD. 2018. Molt in Neotropical birds: Life history and aging criteria. *Studies in*
527 *Avian Biology* 51.
- 528 Johnson OW. 1985. Timing of primary molt in first-year golden-plovers and some evolutionary
529 implications. *Wilson Bulletin* 97:237–239.
- 530 Kiat Y, Izhaki I. 2016. Why renew fresh feathers? Advantages and conditions for the evolution
531 of complete post-juvenile moult. *Journal of Avian Biology* 47:47–56.
- 532 Kiat Y, Izhaki I, Sapir N. 2019. The effects of long-distance migration on the evolution of moult
533 strategies in Western-Palearctic passerines. *Biological Reviews* 94:700–720.
- 534 Marra PP, Cohen EB, Loss SR, Rutter JE, Tonra CM. 2015. A call for full annual cycle research
535 in animal ecology. *Biology Letters* 11 (8): [https://doi.org/ 10.1098/rsbl.2015.0552](https://doi.org/10.1098/rsbl.2015.0552).
- 536 McGuire JA, Witt CC, Remsen JV Jr, Corl A, Rabosky DL, Altshuler DL, Dudley R. 2014.
537 Molecular phylogenetics and the diversification of hummingbirds. *Current Biology* 24:1–
538 7.
- 539 Mulyani YA, Tirtaningtyas FN, Hadi NK, Dewi LK, Kaban A. 2017. Molt in birds inhabiting a
540 human-dominated habitat. *Hayati Journal of Biosciences* 24:195–200.
- 541 Ortiz-Crespo FI. 1972. A new method to separate immature and adult hummingbirds. *The Auk*
542 89:851–857.
- 543 Panter CT. 2021. Sex and age differences in the diet of the Eurasian Sparrowhawk (*Accipiter*
544 *nisus*) using web - sourced photographs: exploring the feasibility of a new citizen science
545 approach. *Ibis*: doi:10.1111/ibi.12918
- 546 Powers DR, Wethington SM. (2020). Broad-billed Hummingbird (*Cyananthus latirostris*), version
547 1.0. In Poole A, Gill FB, editors. *Birds of the World*. Ithaca (NY): Cornell Lab of
548 Ornithology. <https://birdsoftheworld.org/bow/species/brbhum/1.0/introduction>

- 549 Pyle P. 1997. Identification guide to North American birds, part 1. Bolinas (CA): Slate Creek
550 Press.
- 551 Pyle P. 1998. Eccentric first-year molts in certain tyrannid flycatchers. *Western Birds* 29:29–35.
- 552 Pyle P. 2008a. Birding by feather: A molt and plumage primer. *Birding* 40:181–186.
- 553 Pyle P. 2008b. Identification guide to North American birds, part 2. Point Reyes Station (CA):
554 Slate Creek Press.
- 555 Pyle P. 2013. Evolutionary implications of synapomorphic wing-molt sequences among falcons
556 (Falconidae) and parrots (Psittaciformes). *The Condor* 115:593–602.
- 557
- 558 Pyle P, Engilis A Jr., Kelt DA. 2015. Manual for ageing and sexing the landbirds of Bosque
559 Fray Jorge National Park and north-central Chile, with notes on range and breeding
560 seasonality. *The Occasional Papers of the Louisiana State University Museum of Natural*
561 *Science, Special Publications*. <http://www.museum.lsu.edu/occpap.html>
- 562 Pyle P, Howell SNG, Yanega GM. 1997. Molt, retained flight feathers and age in North
563 American hummingbirds. In: Dickerman RW, editor. *The era of Allan Phillips: A*
564 *Festschrift*. Albuquerque (NM): Horizon Communications; p. 155–166.
- 565 Pyle, P, Tranquillo K, Kayano K, Arcilla N. 2016. Molt patterns, age criteria, and molt-breeding
566 overlap in American Samoan landbirds. *Wilson Journal of Ornithology* 128:56–69.
- 567 Rohwer S, Butler LK, Froehlich D. 2005. Ecology and demography of east-west differences in
568 molt scheduling of Neotropical migrant passerines. In: Greenberg R, Marra PP, editors.
569 *Birds of two worlds: The ecology and evolution of migratory birds*. Baltimore (MD):
570 Johns Hopkins University Press; p. 87–105.
- 571 Rohwer S, Ricklefs RE, Rohwer VG, Coppole MM. 2009. Allometry of the duration of flight
572 feather molt in birds. *PLoS Biology* 7:1246.

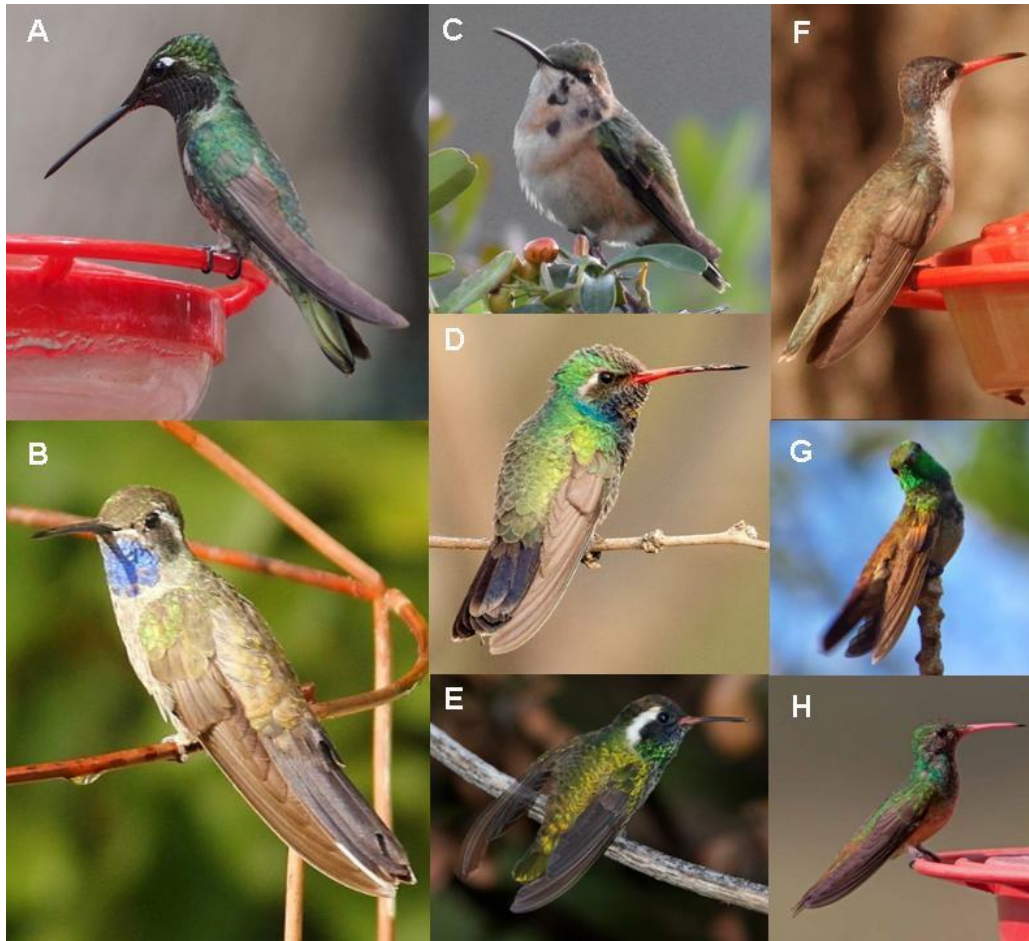
- 573 Rohwer S, Irwin DE. 2011. Molt, orientation, and avian speciation. *The Auk* 128:419–425.
- 574 Rohwer S, Hobson KA, Yang S. 2011. Stable isotopes (δD) reveal east–west differences in
575 scheduling of molt and migration in Northern Rough-winged Swallows. *The Auk*
576 128:622–530.
- 577 Shugart GW, Rohwer S. 1996. Serial descendant primary molt or Staffelmauser in Black-
578 crowned Night Herons. *The Condor* 98:222–233.
- 579 Sieburth D, Pyle P. 2018. Evidence for a prealternate molt-migration in the Rufous
580 Hummingbird and its implications for the evolution of molts in Apodiformes. *The Auk:*
581 *Ornithological Advances* 135:495–505.
- 582 Stiles FG. 1995. Intraspecific and interspecific variation in molt patterns of some tropical
583 hummingbirds. *The Auk* 112:118–132.
- 584 Stiles FG, Remsen JV Jr., McGuire JA. 2017. The generic classification of the Trochilini (Aves:
585 Trochilidae): Reconciling classification with phylogeny. *Zootaxa* 4353:401–424.
- 586 Sullivan BL., Wood, CL, Illif MJ, Bonney RE, Fink D, Kelling S. 2009. eBird: A citizen-based
587 bird observation network in the biological sciences. *Biological Conservation* 142:2282–
588 2292.
- 589 Terrill RS, Seeholzer GF, Wolfe JD. 2020. Evolution of breeding plumages in birds: A multiple-
590 step pathway to seasonal dichromatism in New World warblers (Aves: Parulidae).
591 *Ecology and Evolution*: <https://doi.org/10.1002/ece3.6606>.
- 592 Viera BP, Furness RW, Nager RG. 2017. Using field photography to study avian moult. *Ibis*
593 159:443–448.
- 594 Voelker G, Rohwer S. 1998. Contrasts in the scheduling of molt and migration in eastern and
595 western Warbling Vireos. *The Auk* 115:142–155.
- 596 Wagner HO. 1955. The molt of hummingbirds. *The Auk* 72:286–291.

- 597 Wagner HO. 1957. The molting periods of Mexican hummingbirds. *The Auk* 74:251–257.
- 598 Weidensaul S, Robinson TR, Sargent RR, Sargent MB, Zenzal TJ. 2020. Ruby-throated
599 Hummingbird (*Archilochus colubris*), version 1.0. In Rodewald PG, editor. *Birds of the*
600 *World*. Ithaca (NY): Cornell Lab of Ornithology. <https://doi.org/10.2173/bow.rthhum.01>
- 601 Wethington SM. 2020. Violet-crowned Hummingbird (*Amazilia violiceps*), version 1.0. In Poole
602 AF, Gill FB, editors. *Birds of the World*. Ithaca (NY): Cornell Lab of Ornithology.
603 <https://doi.org/10.2173/bow.vichum.01>
- 604 Williamson FSL. 1956. The molt and testis cycle of the Anna Hummingbird. *The Condor*
605 58:342–366.
- 606 Williamson SL. 2002. *Hummingbirds of North America*. Boston (MA): Houghton Mifflin
607 Company.
- 608 Wolfe JD, Pyle P, Ralph CJ. 2009. Breeding seasons, molt patterns, and gender and age criteria
609 for selected northeastern Costa Rican resident landbirds. *Wilson Journal of Ornithology*
610 121:556–567.
- 611 Yanega GM., Pyle P, Geupel GR. 1997. The timing and reliability of bill corrugations for ageing
612 hummingbirds. *Western Birds* 28:13–18.
- 613 Zimmer JT. 1950. *Studies of Peruvian birds* 56: The genera *Eutoxeres*, *Campylopterus*,
614 *Eupetomena*, and *Florisuga*. *American Museum Novitates* 1450:1–14.



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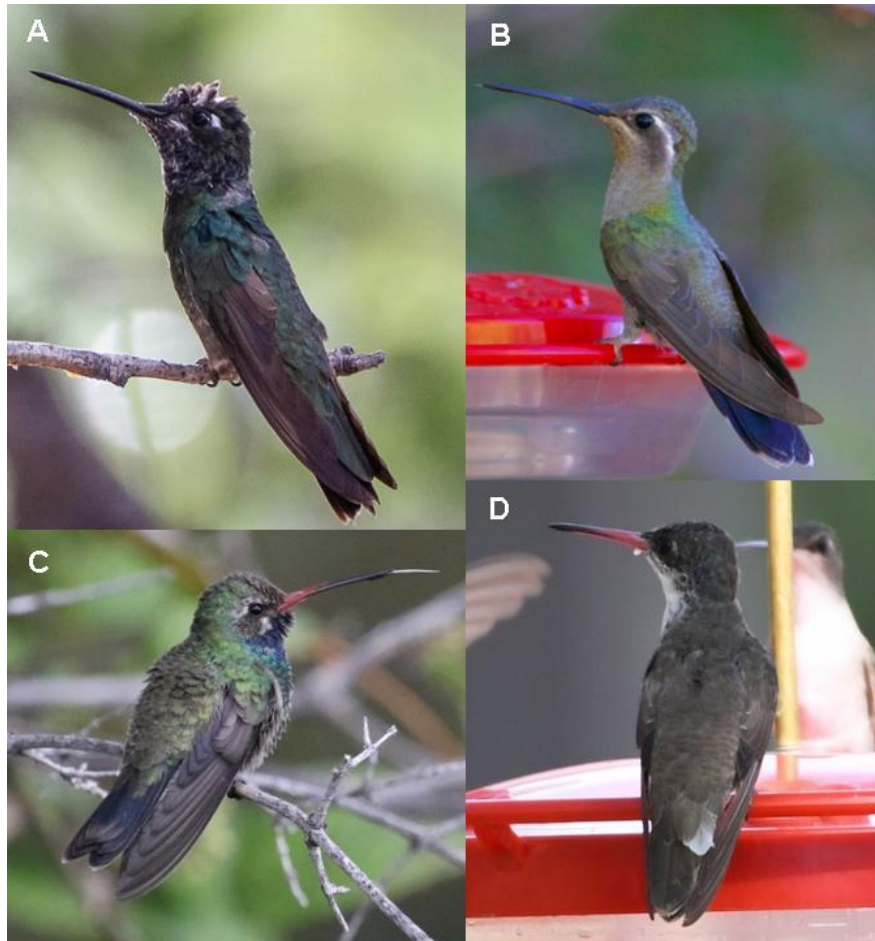
583 **Figure 1. The timing of molt in eight species of hummingbirds that breed in the**
584 **southwestern United States.** Bars represent proportion of the entire monthly sample that were
585 undergoing each molt; see Supplemental Material Table S1 for specific sample sizes for each
586 species by month.



587

588 **Figure 2. Examples of formative plumage in eight species of hummingbirds that breed in**
589 **the southwestern United States. (A)** Rivoli's Hummingbird (*Eugenes fulgens*), 4 Aug 2019;
590 **(B)** Blue-throated Mountain-gem (*Lamphornis clemenciae*), 4 Aug 2012; **(C)** Lucifer
591 Hummingbird (*Calothrax lucifer*), 5 Oct 2009; **(D)** Broad-billed Hummingbird (*Cyananthus*
592 *latirostris*), 2 May 2019; **(E)** White-eared Hummingbird (*Basilinna leucotis*), 5 Aug 2008: **(F)**
593 Violet-crowned Hummingbird (*Leucolia violiceps*), 6 Mar 2016; **(G)** Berylline Hummingbird
594 (*Saucerottia beryllina*), 11 Feb 2017; and **(H)** Buff-bellied Hummingbird (*Amazilia*
595 *yucatanensis*), 26 Apr 2017. Except for White-eared Hummingbird, note the retained juvenile
596 primaries, worn brown secondaries, and molt limits among upperwing secondary coverts in most
597 or all images. The White-eared Hummingbird **(E)** is finalizing a complete preformative molt
598 (aged by dull bill color) after which formative plumage resembles definitive basic plumage in

599 appearance. Photos cropped for enlarged presentation and used by license agreement from the
600 Macaulay Library © Gjon Hazard (**A**, [ML171639201](#)), Ken Murphy (**B**, [ML53554351](#)), Ed
601 Thomas (**C**, [ML168356961](#)), Philip Kline (**D**, [ML156749041](#)), Bill Hubick (**E**, [ML188765291](#)),
602 Debby Parker (**F**, [ML25520031](#)), William Proebsting (**G**, [ML49162901](#)), and Joshua Covill (**H**,
603 [ML56665951](#)).
604



605

606 **Figure 3. Incomplete (arrested or suspended) preformative molts in four species of**
607 **hummingbirds that breed in the southwestern United States. (A) Rivoli's Hummingbird**
608 **(*Eugenes fulgens*), 26 May 2018, having replaced p1-p3; (B) Blue-throated Mountain-gem**
609 **(*Lamphornis clemenciae*), 4 Aug 2012 having replaced p1-p4; (C) Broad-billed Hummingbird**
610 **(*Cynanthus latirostris*), 16 September 2019, having replaced p1-p4; and (D) Violet-crowned**
611 **Hummingbird (*Leucolia violiceps*), 31 Aug 2019 replacing p1-p6. Photos cropped for enlarged**
612 **presentation and used by license agreement from the Macaulay Library © Lydie Mason Warner**
613 **(A, [S46054488](#)), Gordon Atkins (B, [ML101073691](#)), Russ Morgan (C, [S59856736](#)), and Max**
614 **Leibowitz (D, [S59412857](#)).**