



RESEARCH ARTICLE

Evidence for a prealternate molt-migration in the Rufous Hummingbird and its implications for the evolution of molts in Apodiformes

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Submitted December 3, 2017; Accepted February 15, 2018; Published May 2, 2018

ABSTRACT

An inserted body-feather molt has recently been documented in the Ruby-throated Hummingbird (*Archilochus colubris*) during its southbound migration; however, it is unknown whether other species of hummingbirds undergo similar inserted molts or molt-migrations. We examined 346 specimens of Rufous Hummingbird (*Selasphorus rufus*) collected throughout its range and found evidence for a previously unrecognized, inserted body-feather molt that appears to occur, at least partially, at stopover locations in California and the Mexican monsoonal region. This limited molt occurs in all young and in most (but not all) adult Rufous Hummingbirds, primarily in late June through October, before the complete overwinter molt in February–March. The location, timing, and extent of this molt in the crown, back, and underpart tracts showed similar patterns among the 4 age–sex groups; however, patterns of inserted throat-feather molt differed, occurring in all young birds and some adult females but not in adult males. In young birds, replacement of throat feathers preceded that of other body-feather tracts, a pattern that we also found in young male Anna’s Hummingbirds (*Calypte anna*). We suspect that the unusual structure of the gorget feathers in males and the importance of these feathers to territorial defense and mate selection has resulted in these sex-specific patterns. We compare the molts of Ruby-throated and Rufous hummingbirds with those of more basal hummingbird genera and swifts. Based on the most parsimonious interpretation of presumed homologies, we propose that the summer–fall body-feather molts in these hummingbirds are inserted and include a limited preformative molt in young birds and an absent-to-limited definitive prealternate molt in older birds; we consider the first complete molt on the winter grounds to be the second prebasic molt. This terminology appears to best preserve homology during the evolution of both first-cycle and definitive-cycle molts from those of ancestral apodiform taxa.

Keywords: Anna’s Hummingbird, inserted molt, molt-migration, molt terminology, Rufous Hummingbird

Evidencia de una muda migratoria pre-alternativa en *Selasphorus rufus* y sus implicancias para la evolución de las mudas en los Apodiformes

RESUMEN

Una muda insertada de las plumas del cuerpo ha sido recientemente documentada en *Archilochus colubris* durante su migración hacia el sur; sin embargo, no se conoce si otras especies de picaflor experimentan mudas insertadas similares o mudas migratorias. Examinamos 346 especímenes de *Selasphorus rufus* colectados a través de su rango y encontramos evidencia de una muda insertada de las plumas del cuerpo previamente desconocida que parece producirse, al menos parcialmente, en sitios de parada en California y la región monzónica de México. Esta muda limitada se produce en todos los jóvenes y en la mayoría (pero no todos) de los adultos de *S. rufus*, principalmente desde fines de junio hasta octubre, antes que la muda completa de invierno en febrero y marzo. La ubicación, el tiempo y la extensión de esta muda en la corona, la espalda y las partes inferiores mostraron patrones similares entre los 4 grupos de edad/sexo; sin embargo, los patrones de la muda insertada de las plumas de la garganta difirieron, produciéndose en todas las aves jóvenes y algunas hembras adultas pero no en los machos adultos. En las aves jóvenes, el reemplazo de las plumas del cuello precedieron el de las plumas de otras partes del cuerpo, un patrón que también encontramos en los jóvenes macho de *Calypte anna*. Sospechamos que la estructura inusual de las plumas de la gorguera en los machos y la importancia de estas plumas para la defensa territorial y la selección de la pareja ha dado como resultado estos patrones específicos de los sexos. Comparamos las mudas de *A. colubris* y *S. rufus* con la de los picafloros y vencejos de géneros más basales. Basados en la interpretación más parsimoniosa de presuntas homologías, proponemos que las mudas de verano-otoño de las plumas del cuerpo en estos picafloros son insertadas e incluyen una muda limitada pre-formativa en las aves jóvenes y una muda definitiva pre-alternativa ausente a limitada en las aves más viejas; consideramos que la primera muda completa en los sitios de invernada son la segunda muda pre-básica. Esta terminología parece preservar mejor la homología durante la evolución de las mudas del primer ciclo y del ciclo definitivo a partir de aquellas de un taxa Apodiforme ancestral.

Palabras clave: *Calypte anna*, migración-muda, muda insertada, *Selasphorus rufus*, terminología de la muda

INTRODUCTION

It has been widely reported that migratory North American hummingbirds undergo complete molts on the winter or nonbreeding grounds, both in postbreeding adults and during the first winter after hatching (Aldrich 1956, Williamson 1956, Oberholser 1974, Pyle 1997, Pyle et al. 1997, Howell 2010). Following the terminology of Howell et al. (2003), these have been considered complete prebasic and preformative molts, respectively. First-year males of most species are also known to replace at least a few throat feathers during the first fall, which are later replaced again during the preformative molt (Baltosser 1995, Pyle et al. 1997). The replacement of these throat feathers has been regarded as part of an inserted “first presupplemental” or auxiliary preformative molt (see Pyle 1997, 2008, Howell et al. 2003, Howell 2010, Weidensaul et al. 2013).

More recently, Dittmann and Cardiff (2009) documented an additional inserted molt within the definitive cycle of the Ruby-throated Hummingbird (*Archilochus colubris*). In late summer, these hummingbirds undergo a molt-migration to southeastern North America for a partial molt that includes a variable number of body feathers, up to most or all in some birds, but no wing coverts or flight feathers (Dittmann and Cardiff 2009, Weidensaul et al. 2013). These feathers are replaced again during late winter. Dittmann and Cardiff (2009) also documented body-feather replacement in first-fall birds of both sexes on molting grounds, in addition to the throat feathers of males, prior to the first complete molt. These inserted molts in the Ruby-throated Hummingbird suggest that molt cycles may be more complex in hummingbirds than previously thought. In North America, migratory species of birds usually show more inserted molting than nonmigratory species (Pyle 1997, 2008, Howell 2010), so it seems reasonable to expect that inserted prealternate molts may also occur in other migratory North American hummingbird species.

The Rufous Hummingbird (*Selasphorus rufus*) breeds in April–July, from southeastern Alaska (61°N) to northern California and inland to central Idaho and Montana, and it winters primarily in south-central Mexico (Healy and Calder 2006). Spring migration primarily occurs between late February and May, and fall migration occurs between late June and September, with first-fall birds migrating 20–30 days later than older birds, on average (Phillips 1975, Howell and Gardali 2003). During fall migration, Rufous Hummingbirds use “stopover” locations with flower blooms in California and Arizona for refueling (Russell et al. 1994, Healy and Calder 2006). Given their similar long-distance migration strategies, we investigated whether the Rufous Hummingbird undergoes an inserted molt at stopover

locations during southbound migration similar to that documented in the Ruby-throated Hummingbird.

METHODS

We examined 346 specimens of Rufous Hummingbird, housed at the California Academy of Sciences (CAS), San Francisco; the Museum of Vertebrate Zoology (MVZ), Berkeley; and the Moore Laboratory of Zoology (MLZ), Los Angeles, California, USA. Specimens were collected between 1883 and 2010. Specimens at CAS ($n = 109$) and MVZ ($n = 162$) were collected primarily in Alaska through California, on the breeding grounds or during migration, whereas specimens from MLZ ($n = 75$) were collected primarily in Mexico, during migration, at stopover locations, or on the wintering grounds. We determined the age and sex of each specimen following the criteria of Pyle (1997) along with information on specimen labels. From June through March, before completion of the overwinter molt, birds were aged as either in their first cycle (hereafter “young”) or definitive cycle (hereafter “adult”), based on bill corrugations, feather wear, and plumage characteristics such as the extent of iridescent red to orange feathers in the throat and the color pattern of the central rectrices. Among young birds, males and females were distinguished primarily by the amount of rufous in the central rectrices and bronze spotting to the throat, along with the widths of outer primaries and rectrices (Pyle 1997). Specimen labels accorded with our sex determinations of young birds in most cases; we attributed a few conflicts to mis-sexing during specimen preparation. For birds collected following completion of the overwinter molt, during February–May, the molt cycle could no longer be determined, and all birds were considered “adults.” In order to further assess and compare patterns of molt in young Rufous Hummingbirds, we also examined 54 specimens of young male Anna’s Hummingbirds (*Calypte anna*) located at CAS, collected between March 19 and October 30, prior to commencement of the first primary molt.

We examined specimens for signs of active molt at the time of collection or for mixed generations of feathers, indicating a prior limited or partial molt. We examined plumage in the feather tracts of 4 body-feather regions: the crown, back, underparts, and throat. Feathers of the throat included those with bright iridescent tips, part of the gorget of Rufous Hummingbird. New iridescent feathers in the throat were counted in young birds. For many specimens, voucher photographs were taken for later confirmation and analysis (Figure 1). We scored each region as follows: uniform, mixed (2 generations of feathers), or molting. Regions that were scored as uniform appeared to have all feathers replaced during the same molt. Regions were considered to have been actively

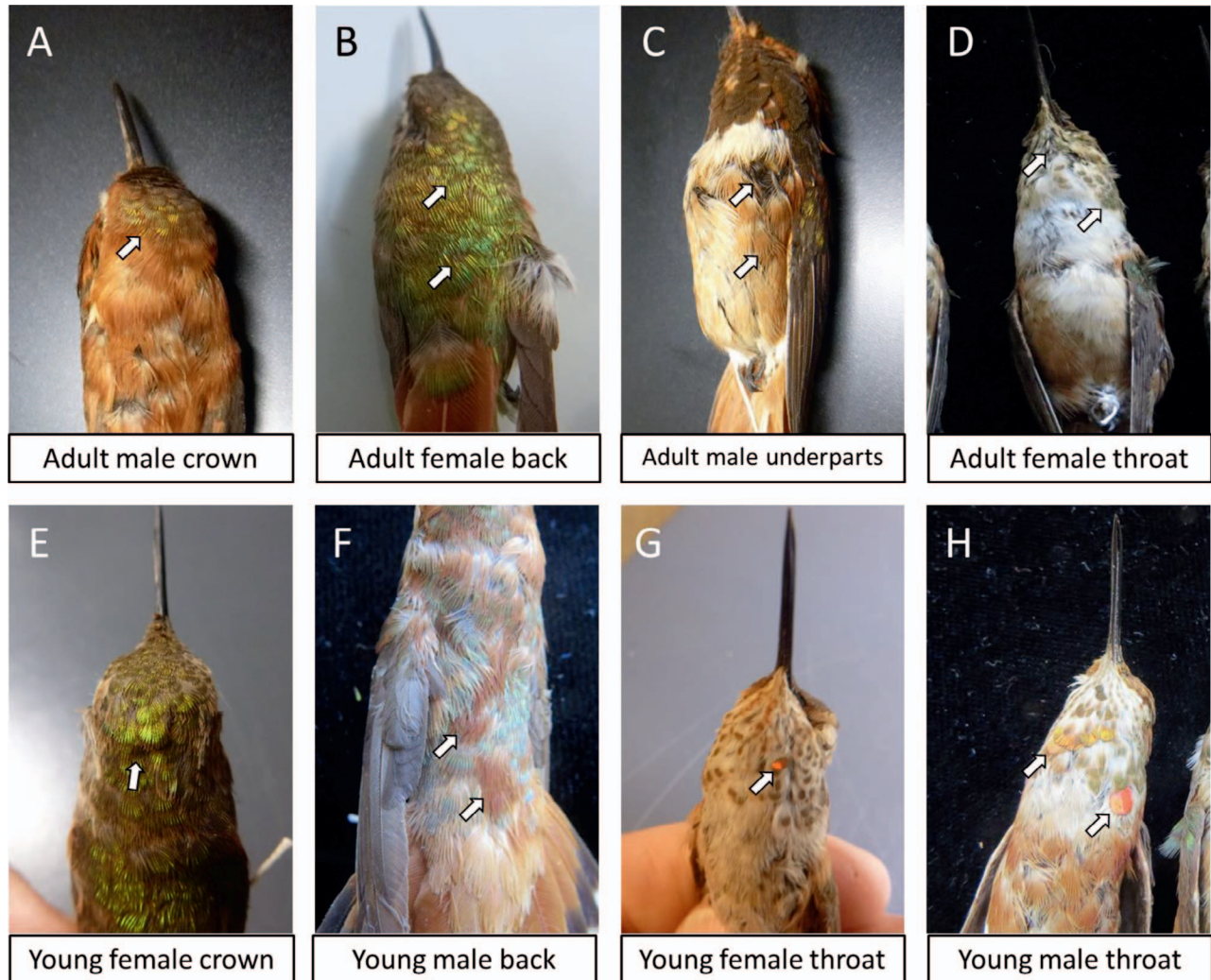


FIGURE 1. Representative images of Rufous Hummingbirds showing evidence of previous body-feather molt. Arrows point to examples of newly molted feathers. (A) Adult male, showing incoming orange feathers interspersed with the green feathers in the crown (CAS 39461, Cochise County, Arizona, July 15, 1896). (B) Adult female, showing replaced green feathers in the back (MVZ 127422, Bower County, Idaho, July 20, 1916). (C) Adult male, showing new incoming orange feathers and missing feathers in the underparts (CAS 39461, Cochise County, Arizona, July 15, 1896). (D) Adult female, showing incoming green feathers and pinfeathers on the throat (MLZ 46372, Durango, Mexico, July 27, 1947). (E) Young female showing missing and incoming green feathers in the crown (CAS 96927, San Francisco, California, September 2, 2008). (F) Young male, showing incoming orange feathers in the back (MLZ 13412, State of Mexico, Mexico, October 22, 1932). (G) Young female, showing an incoming red feather in the throat (CAS 75808, Cochise County, Arizona, August 10, 1893). (H) Young male, showing incoming orange feathers in the throat (MLZ 13412, Mexico, Mexico, October 22, 1932).

molting if there were pinfeathers or sheathed feathers present. We considered a bird to be showing evidence of an inserted molt if there were any molting or mixed feathers present in any region between June and March, prior to initiation of the complete winter–spring body-feather molt in February or March. We also inspected each specimen for signs of replaced primaries, which occurred in distal sequence (except for the outer 2 primaries) typical of hummingbirds (Pyle 1997). We assigned each specimen a primary score of 0–10, indicating how many primaries had

been recently replaced or were growing at the time of collection.

RESULTS

We examined 153 Rufous Hummingbird specimens collected in February–May and following completion of the overwinter molt. All 153 showed uniform feathers in all tracts, with feather wear indicating complete replacement of body feathers during this molt. The remaining 193

TABLE 1. Sample size of Rufous Hummingbirds collected prior to completion of the overwinter molt, by 2 mo period.

Age–sex	June–July	August–September	October–November	December–January	February–March	All months
Adult male	36	8	1	4	0	49
Adult female	21	19	3	7	5	55
Young male	12	25	2	3	3	45
Young female	16	21	4	1	2	44
All ages–sexes	85	73	10	15	10	193

specimens were collected in June–March and prior to completion of the overwinter molt. These consisted of 49 adult males, 55 adult females, 45 young males, and 44 young females (Table 1). Among these specimens, we found evidence of a limited body-feather molt in all 4 age–sex groups during fall and winter, prior to initiation of the primary molt (Figures 1 and 2).

Among 104 adults collected in June–March, prior to completion of primary molt, evidence of body-feather molt occurred in 37% of 57 individuals collected in June–July, 71% of 42 individuals in August–January, and 80% of 5 individuals in February–March, with the proportion not appearing to change substantially between August and January (Figure 2A). The earliest signs of this molt were observed in a male collected in Nevada on June 29 with mixed feathers in the upperparts and underparts (MVZ 65214), whereas 13 other adults collected in June lacked evidence of molt. Only 14 of 104 adults were recorded with actively molting body feathers, 7 between July 8 and September 24, one in December, and 4 between February 16 and March 26. These results indicate that body-feather replacement occurred primarily in late June through September, after which little or no molt in these regions occurred until that accompanying the complete overwinter molt in February–March (the December bird showing pinfeathers may have been undergoing adventitious feather replacement). The temporal pattern of replacement (Figure 2A) suggests that this molt may begin on or near breeding grounds but occurs primarily during migration at stopover locations. The molt appears to include fewer feathers of the crown than those of the back and underparts (Figures 1A–1D and 2A). Our data also suggest that some adults, perhaps 30–35% of individuals, do not replace body feathers in July–September. With the exception of throat feathers (see below), we found no differences among adults in the timing or proportions of body feathers replaced between males and females.

We also found evidence of body-feather molt in all 4 regions of young birds (Figures 1E–1H and 2B), although the temporal pattern of replacement appeared to differ from that of adults. Throat feathers began to be replaced in July and continued to be replaced through November or December, whereas feathers of the crown, back, and underparts were replaced primarily in September–Novem-

ber (Figure 2B). The earliest evidence of molt in the throat was shown by a young female collected on July 1 in British Columbia with 2 throat feathers replaced (MVZ 102010), whereas the earliest signs of molt in the other body regions was shown by a young female collected on July 31 in Durango, Mexico, with back feathers replaced (MLZ 46358). Furthermore, among 56 young birds undergoing fall migration and collected in California, 57% showed mixed throat feathers but only one individual, a female collected in San Francisco on September 2 (Figure 1E), showed molt in other body-feather regions. This suggests that throat-feather molt can commence on or near breeding grounds and continue during migration or at stopover locations in young birds, whereas molt in other body-feather regions, along with continued molt of throat feathers, occurs primarily at stopover sites in Arizona and northern Mexico (Figure 2B). In contrast to adults, birds collected in February–March within our sample had not yet commenced the overwinter body-feather molt. Our data suggest that all young birds replace throat feathers prior to the overwinter molt but, as in adults, fewer crown feathers than upperpart and underpart feathers were replaced, and perhaps 30–35% of birds did not appear to undergo molt in these regions during this period. As with adults, we found differences between the sexes in throat-feather molting patterns (see below) but not in the feathers of the other regions; indeed, the extent of molt in the 3 body-feather regions other than the throat appeared to be similar among all 4 age–sex groups (Figure 2A, 2B).

Specimens of birds undergoing molt of primaries were collected in Mexico between October 10 (MLZ 29590) and March 4 (MLZ 27617); birds collected between those dates (i.e. during March–October) had replaced all 10 primaries. Among all 4 age–sex groups, we found little change in overall proportion of birds showing body-feather molt in the crown, back, and/or underparts during progression of the primary molt (Figure 2C). This indicates little or no body-feather molt during the period of primary molt, although commencement of the complete overwinter body-feather molt can occur in adults in February–March, toward the end of the primary molt, as noted above. The lack of mixed feathers in birds collected in February–May and following the complete overwinter molt indicates that all replaced body feathers in all 4 age–sex groups are replaced again during the overwinter molt, confirming the

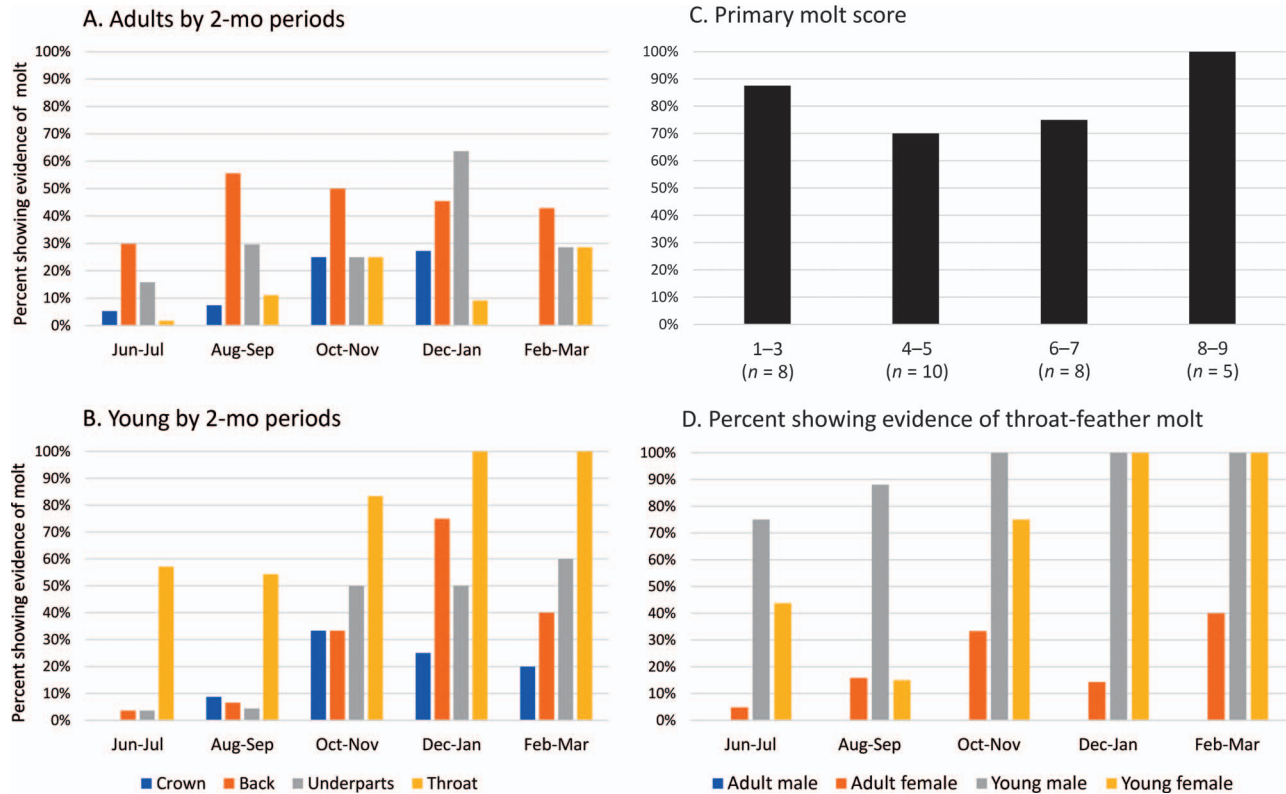


FIGURE 2. Proportion of (A) adult and (B) young Rufous Hummingbirds showing evidence of prior body-feather molt (mixed generations of feathers) in the crown, back, underparts, and throat; (C) proportion of Rufous Hummingbirds (of both age groups) showing evidence of previous body-feather molt according to primary molt score (i.e. the proportion of individuals showing molt in any of the crown, back, or underparts); and (D) proportion of Rufous Hummingbirds showing evidence of throat-feather molt according to age and sex. Sample sizes are presented in Table 1.

presence of a limited, inserted body-feather molt, primarily in June through November or December.

Patterns of throat-feather replacement during the summer–fall molt showed substantial differences among the 4 age–sex groups (Figure 2D). Among adults, we found no males that had replaced throat (including iridescent gorget) feathers during summer and fall, indicating that these feathers are replaced only once per year, during the overwinter molt. Adult females did show new throat feathers, apparently replaced primarily in July–September as in the other body-feather regions (Figure 2A); new feathers were primarily to the sides of the existing iridescent gorget feathers, and they all lacked iridescence (Figure 1D). Among young birds, a higher proportion of males than of females showed throat-feather replacement earlier during the summer–fall period, until December, by which time all birds of both sexes showed at least a few new throat feathers (Figure 2D). All new throat feathers in young males showed iridescent tips. Young females showed smaller iridescent areas to feathers replaced in the center of the throat, whereas feathers to the sides lacked iridescence (Figure 1G, 1H), mimicking the plumage pattern of adult females. Young males also

showed larger numbers of throat feathers replaced than females at a given time within the molting season (Figure 3).

Our sample of Rufous Hummingbird specimens included no nestlings and few or no recently fledged young collected in June, so we also examined 54 specimens of young male Anna's Hummingbirds collected prior to commencement of the first primary molt, which occurs during July–February (Pyle 1997). Body-feather replacement in young male Anna's Hummingbirds showed patterns similar to those in Rufous Hummingbirds, with an apparent molt occurring before commencement of primary molt, and throat-feather replacement commencing before that of other body-feather tracts (Figure 4A). By May, 90% of males had replaced throat feathers, but only 30% had renewed crown, back, and/or underpart feathers (Figure 4A). Furthermore, only 13% of specimens showed signs of molt in these 3 body-feather regions when <6 throat feathers had been replaced, whereas 100% of specimens that had replaced >10 throat feathers had signs of molt in these regions (Figure 4B). The sample included 6 nestlings or recently fledged juvenile males collected between March 19 and May 16, none of which

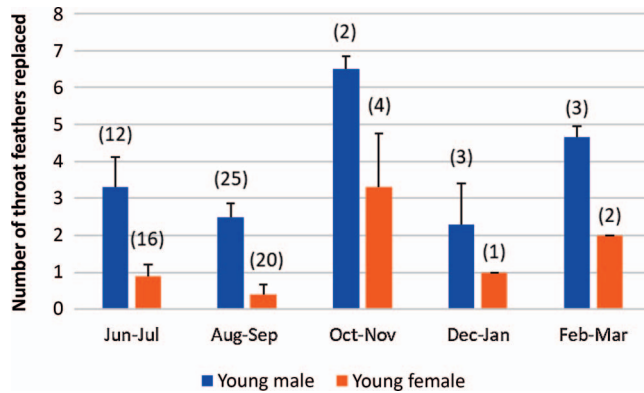


FIGURE 3. Mean numbers (\pm SE) of iridescent throat feathers replaced in young male and female Rufous Hummingbirds, June–March. New central throat feathers in young females had small, red, iridescent centers, and new throat feathers in young males had larger, bright orange centers. Ranges of replaced feathers were 0–11 feathers in males and 0–8 feathers in females.

showed replaced throat or body feathers. It thus appears that young male Anna's Hummingbirds have an inserted molt similar to that of young male Rufous Hummingbirds, commencing with throat feathers; all birds replaced throat and underpart feathers, and most renewed crown and back feathers prior to commencement of the primary molt.

DISCUSSION

An Inserted Molt in Rufous Hummingbird

Our results indicate that most Rufous Hummingbirds of all 4 age–sex groups undergo a limited inserted body-feather molt during July–December. In postbreeding adults, feather replacement appeared to begin on or near the breeding grounds in late June or early July, continued after molt-migration to stopover locations, and had completed by October or November, presumably before winter grounds are reached (cf. Phillips 1975). In postfledging young birds, the molt of tracts other than the throat appeared to commence in late September and October at stopover locations and continued through November or December. These inserted molts may have evolved in order to replace feathers that had become worn due to the migratory habits and increased solar exposure that are experienced by Rufous and Ruby-throated hummingbirds (and not by less migratory hummingbird species) on an annual basis.

Molt of throat feathers occurred in all young birds but more extensively in males than in females; among adults, no evidence of throat-feather replacement was observed in males, whereas $\leq 30\%$ of adult females molted a few throat feathers during this period. Our results indicate that young male Anna's Hummingbirds also show replacement patterns in the throat and other tracts similar to those in

young male Rufous Hummingbirds. Such substantial sex-specific variation in molt patterns is unusual in birds, being found predominantly in ptarmigan and ducks (Pyle 2005, 2007), with some first-year males of some passerine species showing more replacement during first prealternate molts than other age–sex groups (Pyle 1997). Male Rufous Hummingbirds use their iridescent gorget for territorial display directed toward other males (Hurly et al. 2001). In adult males, full gorget feathers might be expensive to produce and may not lose enough of their function with wear to be worth replacing during the summer–fall molt. Renewed throat feathers are fuller in adult males than in young males (Pyle et al. 1997), influenced, perhaps, by decreased nutrition in the latter (Meadows et al. 2012), and may thus be less expensive to produce. Yet it may also be important for young males to show these feathers for territorial purposes at stopover locations and on the winter grounds, where Rufous Hummingbirds defend territories in areas with high densities of flowers (Kodric-Brown and Brown 1978, Carpenter et al. 1983, Russell et al. 1994). First-fall male hummingbirds with brighter-colored throats and crowns have been shown to spend less time and energy defending their territories than those with less iridescent colors (Ewald and Rohwer 1980), and the earlier timing of throat-feather replacement in young males may address such a need at stopover locations in California (Russell et al. 1994). Throat feathers in female Rufous Hummingbirds, for the most part lacking iridescence, are presumably also less expensive to grow, although young females that molt in a few central throat feathers with iridescent orange patches might also enable them to better defend territories during migration.

Ruby-throated Hummingbirds appear to undergo summer–fall molting patterns similar to those of Rufous Hummingbirds, with the exceptions that adult male Ruby-throated Hummingbirds can replace gorget throat feathers and that a higher proportion of adults may replace a higher proportion of body feathers (Dittmann and Cardiff 2009). As in Rufous Hummingbirds, this molt appears to occur primarily during June–September, starting on the breeding grounds and concluding primarily at stopover locations along the coast of the Gulf of Mexico (cf. Zenzal and Moore 2016). Why adult male Ruby-throated Hummingbirds would replace gorget feathers twice a year, whereas adult male Rufous Hummingbirds replace these feathers only once a year, is a question for further investigation.

Molt-Migration

Some North American passerines migrate to the Mexican monsoon region to undergo molt from July to September, before resuming migration to their wintering grounds in the Neotropics (Rohwer et al. 2005, Pyle et al. 2009). Our results indicate that both adult and young Rufous Hummingbirds may undergo molt at stopover locations

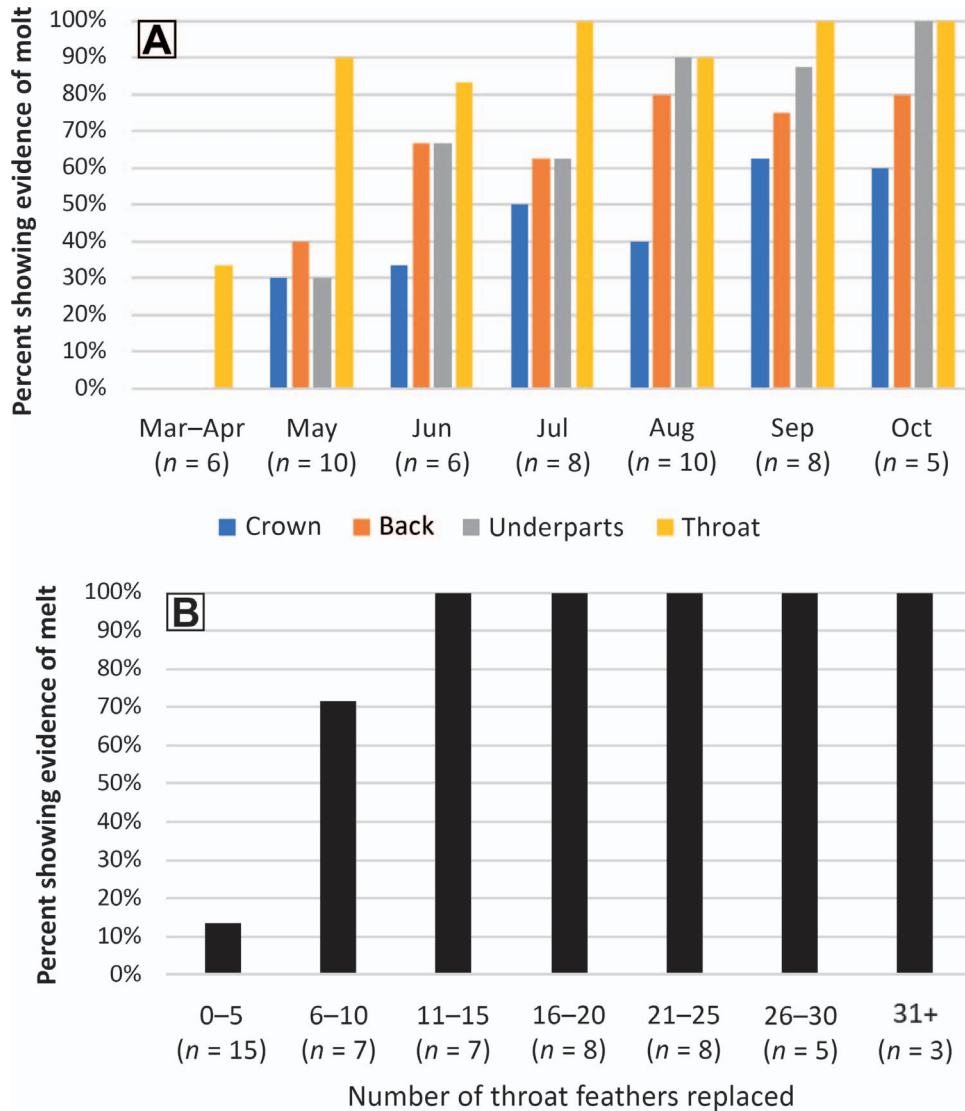


FIGURE 4. Percentages of young male Anna’s Hummingbird specimens ($N = 54$) showing evidence of (A) molt in the crown, back, underparts, and throat, respectively, from March through October; and (B) molt in the crown, upperparts, or underparts in relation to the number of throat feathers replaced.

in California and the Mexican monsoonal area and that the species thus can be regarded as a molt-migrant. We found that 75% of young and 64% of adult Rufous Hummingbirds collected between August and October in northwest Mexico (Sonora, Sinaloa, and Chihuahua) showed evidence of molt in the crown, back, and/or underparts and that 2 of 3 adults collected there in August were in body-feather molt. Rufous Hummingbirds are not known to winter regularly in these areas (Phillips 1975, Healy and Calder 2006), which suggests they may be important stopover molting locations before migration to the winter grounds in south-central Mexico.

Like molt-migrant passerines, Rufous Hummingbirds may be drawn to stopover in the Mexican monsoonal

region to take advantage of the high food availability associated with late-summer monsoonal rains. During the Mexican monsoonal period, flower abundance increases dramatically in the Sierra Madre Occidental of Sonora, involving common flowering plants, such as *Mandevilla foliosa*, *Castilleja patriotica*, and *Stachys coccinea*, that are defended by Rufous Hummingbirds (Van Devender et al. 2004). Other widely scattered plants, including *Cuphea llavea*, *Bouvardia ternifolia*, *Penstemon wislizenii*, *Centaurea rothrockii*, and *Salvia iodantha*, also provide nectar for hummingbirds in the Sierra Madre Occidental in summer, at which time Rufous Hummingbirds are dominant to other migratory North American hummingbirds and were found to take nectar from the greatest

variety of flowers (Van Devender et al. 2004, Lopez-Segoviano et al. 2018).

Although the molt-migration of both Ruby-throated and Rufous hummingbirds involves absent-to-limited body-feather molts rather than the complete prebasic molt or partial-to-incomplete preformative molts as found in other monsoonal molt migrants, molt-migrations for body feathers have been found in other species of birds, such as the preformative molts of some Mexican monsoonal molt-migrants (Pyle et al. 2009) as well as the prealternate molts of shorebirds (Pyle 2008, Lourenço and Piersma 2015) and blackbirds (Wright et al. 2018). As in other monsoonal molt-migrant species, molt-migration in Rufous and Ruby-throated hummingbirds may involve variable and heterogeneous molt-movement responses among individuals, suggesting annual decisions at the individual level based on immediate food-resource conditions on the summer and molting grounds, along with success during the previous breeding season (Pyle et al. 2009).

The Evolution of Hummingbird Molts and Molt Terminology

Our results indicate that the sequences of molts in Rufous and Ruby-throated hummingbirds are rather similar in timing, extent, and location and can be presumed homologous (*sensu* Humphrey and Parkes 1959). Three possible terminologies have been proposed to account for the inserted molts of Ruby-throated Hummingbird (Figure 5A–5C). Dittmann and Cardiff (2009) and Howell (2010) proposed that the summer–fall body-feather molt of adults be considered part of the definitive prebasic molt, followed by completion of this molt with wing-feather replacement, and that the body-feather molt in February–March be considered the definitive prealternate molt (Figure 5A). Howell (2010) extended this scenario to young birds as well, considering the summer–fall body-feather molt and the winter flight-feather molt as the preformative molt, followed by the first prealternate molt in February–March (Figure 5A). This terminology could be plausible in Ruby-throated Hummingbird, especially if the summer body-feather molts were indeed complete in all young and adult birds. However, under this terminology, the presumed homologous preformative and prebasic molts in Rufous Hummingbird would be limited or even absent, followed by complete first and definitive prealternate body-feather molts. This would represent a novel molt strategy in birds, requiring a prebasic body-feather molt to have become less complete evolutionarily and replaced by a more complete prealternate body-feather molt (see also Pyle and Reid 2016). Homology of the prebasic molt cycle between Ruby-throated Hummingbird and other hummingbirds that lack inserted molts could also be lost under this terminology, as there would be no equivalent to the prebasic body-feather

molt in these related species (Weidensaul et al. 2013). For example, if Anna's Hummingbird lacks an inserted molt in adults, as indicated by Williamson's (1956) detailed study, then the definitive prealternate body-feather molt of Ruby-throated and Rufous hummingbirds would appear to be equivalent with the definitive prebasic molt in Anna's Hummingbird, and presumed homology would be lost.

A second scenario mentioned by Dittmann and Cardiff (2009) would apply the summer–fall body-feather molt in adult Ruby-throated Hummingbirds to the definitive prealternate molt, followed by the complete overwinter definitive prebasic molt (Figure 5B). Under this scenario, the summer–fall molt in young birds could be considered an auxiliary preformative molt (Howell et al. 2003, Pyle 2008; formerly known as the “first presupplemental molt”), followed by the complete overwinter preformative molt (Figure 5B). This terminology would maintain presumed homology within the definitive cycle as widely understood for most or all other hummingbird species (e.g., Pyle 1997) and would result in the prebasic body-feather molt following rather than preceding the wing-feather molt, as found in other species of birds with inserted summer–fall molts (Pyle 2005, 2007, 2008; Pyle and Reid 2016). Under this second scenario, however, the auxiliary preformative molt would be unusual in being more extensive in Ruby-throated Hummingbirds than those proposed for most other species (Thompson and Leu 1994, Pyle 1997, 2008), and in having it separated from the preformative body-feather molt by a wing-feather molt. Furthermore, a partial body-feather molt during the first cycle in other hummingbirds is usually considered a preformative molt (Figure 5; see below), and homology could be lost if these molts in Ruby-throated and Rufous hummingbirds are considered auxiliary preformative.

Pyle has proposed a third terminology (see Dittmann and Cardiff 2009, Weidensaul et al. 2013) that would include the same sequence in adults as in the second scenario above; but in young birds, the summer–fall body molt would be considered a partial preformative molt and the complete overwinter molt would be considered the second prebasic molt, pulled forward in time as compared to this molt in most other birds (Figure 5C). The summer–fall inserted molt at ~1 yr of age would become the second prealternate molt. This scenario would maintain homology with the definitive cycle of other migratory North American hummingbirds, as mentioned above, and would also maintain homology with other more basal genera of hummingbirds (cf. McGuire et al. 2014) that appear to have partial preformative molts but lack wing-feather replacement—for example, *Florisuga* (Zimmer 1950), *Topaza* (Hu et al. 2000), *Phaethornis* (Stiles 1980), *Patagonia* (Pyle et al. 2015), *Eugenes* and *Lampornis* (P. Pyle personal observation), and other tropical hummingbirds (Johnson and Wolfe 2018). A possible drawback

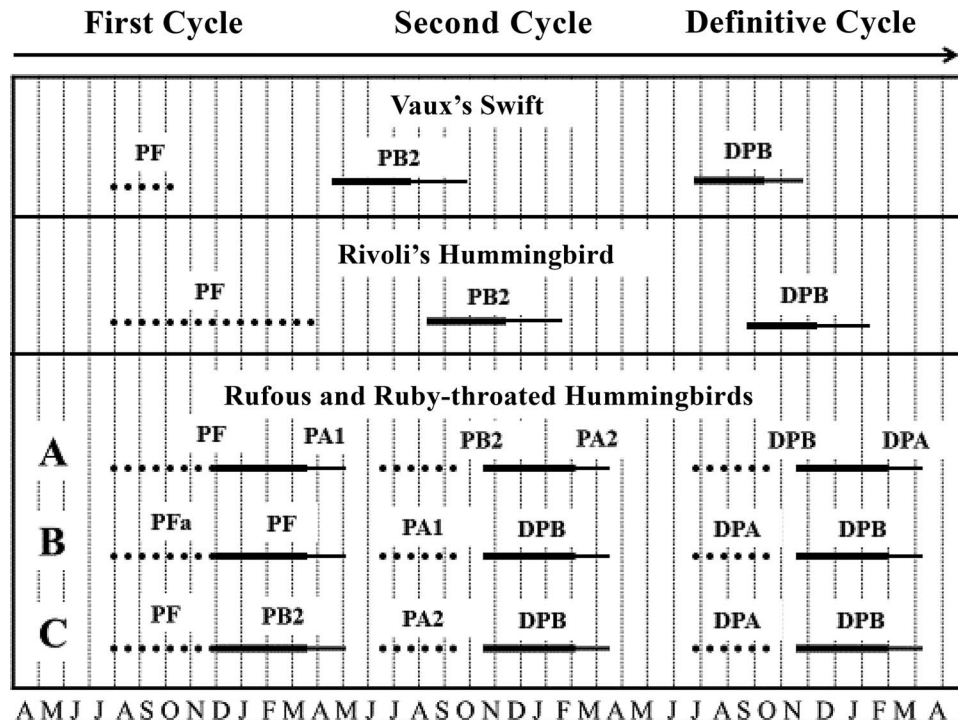


FIGURE 5. Molt strategies and terminology in Vaux’s Swift (*Chaetura vauxi*), Rivoli’s Hummingbird (*Eugenes fulgens*), and Rufous Hummingbird (based on Pyle 1997, personal observation; present study) to assess the evolution of molt homologies and corresponding terminology. Three terminologies for Rufous Hummingbird have been proposed (A–C; see text).

could be that this terminology could represent a novel strategy (as known thus far) in birds (Howell et al. 2003, Howell 2010), in which the first molt cycle has been truncated compared to the definitive molt and breeding cycles, although the prebasic molt can be pulled forward by at least several months because of a lack of breeding constraints (Pyle 2008), as in swifts (Figure 5), for example, and in seabirds and raptors that don’t breed in their first year. In any case, molt terminology should be determined irrespective of breeding regimes (Humphrey and Parkes 1959).

Application of best molt terminology according to the Humphrey and Parkes (1959) system depends on how the molts of Rufous and Ruby-throated hummingbirds have evolved, in this case from those of a common ancestor of hummingbirds and swifts, the latter widely considered a sister group to ancestral hummingbirds (e.g., Prum et al. 2015). Under the first terminology described above (Figure 5A), a definitive prealternate molt would have been inserted into the first and definitive molt cycles, following the prebasic molt; the prebasic body-feather molt would have evolved to become incomplete or absent; and the preformative molt would have evolved to include wing feathers but not all body feathers, as distinct from most birds, including more basal hummingbirds and swifts (Figure 5; Cramp 1985, Pyle 1997, Howell 2010). The second terminology (Figure 5B) could indicate that other

migratory hummingbirds have prealternate molts—a distinct possibility, given how poorly understood the molt strategies of hummingbirds are, including (until recently) those of the otherwise well-studied Ruby-throated Hummingbird. Migratory species of birds are more likely to undergo more complete preformative molts and to have inserted prealternate molts (Howell 2010), presumably because of increased solar exposure on an annual basis (Pyle 1998, 2008). However, under both of these first 2 terminologies, either (1) homology of first-cycle molts would appear to be lost compared to those of more basal hummingbirds and swifts or (2) several steps would be needed, including both insertion and loss of molts evolutionarily, in order to preserve homology. Under the third terminology described above (Figure 5C), both the partial preformative and complete definitive prebasic molts of more basal tropical hummingbirds and swifts are preserved in Rufous and Ruby-throated hummingbirds, and this would appear to be the most parsimonious evolutionary pathway, involving the fewest novel modifications and best preserving molt homologies in these taxa. A better understanding of molt strategies in swifts and additional basal hummingbirds would also help confirm our revised terminology.

We propose that first breeding in ancestral tropical hummingbird species may have become advanced to 4–6 mo postfledging, followed by a complete second prebasic

molt at 5–8 mo postfledging. As migratory hummingbird species later evolved, the shortened molt cycle may have been preserved, while the first breeding attempt was precluded because of the constraints of migration or premature development, as in other species that delay breeding until the second year or later and advance the second prebasic molt. Given the preservation of homology and the possible need for an accelerated breeding and molt cycle in hummingbirds, we believe that the third scenario proposed above (Figure 5C) is the most likely explanation for the evolution of inserted prealternate molts in Rufous and Ruby-throated hummingbirds from those of ancestral apodiform taxa. As such, these species would exhibit a “simple alternate molt strategy” as defined by Howell et al. (2003). Given that the summer–fall molt of young birds appears to be homologous with preformative molts of other hummingbirds, we would consider the single inserted first-cycle molt in Rufous Hummingbird a preformative rather than a first prealternate molt (for discussion on assigning first-cycle molts within the simple alternate molt strategy, see Pyle 2008, Howell and Pyle 2015, Johnson and Wolfe 2018), despite the fact that it appears to be very similar in timing, location, and extent to the definitive prealternate molt according to this terminology. It is possible that the extents, timings, and locations of these inserted molts have been shaped by migration constraints and the other factors mentioned above, despite the definitive prealternate molt having evolved separately. Under this scenario, Rufous Hummingbirds would undergo both a preformative and a definitive prealternate molt-migration, as defined by C. M. Tonra and M. W. Reudink (personal communication).

ACKNOWLEDGMENTS

We thank J. Maley and J. McCormack at the Moore Lab of Zoology, C. Cicero at the Museum of Vertebrate Zoology, and M. Flannery at the California Academy collections for giving us access to these specimens. We also thank D. Sieburth for assisting with the figures and tables.

Funding statement: P.P.'s time for this study was partially funded by the Institute for Bird Populations.

Ethics statement: No ethics protocols were needed to conduct this research.

Author contributions: P.P. conceived the study, P.P. and D.S. collected and analyzed the data, and D.S. and P.P. wrote the manuscript. This is contribution no. 577 of the Institute for Bird Populations.

LITERATURE CITED

Aldrich, E. C. (1956). Pterylography of the Allen Hummingbird. *The Condor* 58:121–133.

Baltosser, W. H. (1995). Annual molt in Ruby-throated and Black-chinned hummingbirds. *The Condor* 97:484–491.

Carpenter, F. L., D. C. Paton, and M. A. Hixon (1983). Weight gain and adjustment of feeding territory size in migrant hummingbirds. *Proceedings of the National Academy of Sciences USA* 80:7259–7263.

Cramp, S. (Editor) (1985). *The Birds of the Western Palearctic*, vol. 4. Oxford University Press, Oxford, UK.

Dittmann, D. L., and S. W. Cardiff (2009). The alternate plumage of the Ruby-throated Hummingbird. *Birding* 41:32–35.

Ewald, P. W., and S. Rohwer (1980). Age, coloration and dominance in non-breeding hummingbirds: A test of the asymmetry hypothesis. *Behavioral Ecology and Sociobiology* 7:273–279.

Healy, S., and W. A. Calder (2006). Rufous Hummingbird (*Selasphorus rufus*), version 2.0. In *Birds of North America Online* (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, New York, USA. <https://birdsna.org/Species-Account/bna/species/rufhum>

Howell, S. N. G. (2010). *Molt in North American Birds*. Houghton Mifflin Harcourt, New York, NY, USA.

Howell, S. N. G., and T. Gardali (2003). Phenology, sex ratios, and population trends of *Selasphorus* hummingbirds in central coastal California. *Journal of Field Ornithology* 74:17–25.

Howell, S. N. G., and P. Pyle (2015). Use of ‘definitive’ and other terms in molt nomenclature: A response to Wolfe et al. (2014). *The Auk: Ornithological Advances* 132:365–369.

Howell, S. N. G., C. Corben, P. Pyle, and D. I. Rogers (2003). The first basic problem: A review of molt and plumage homologies. *The Condor* 105:635–653.

Hu, D.-S., L. Joseph, and D. Agro (2000). Distribution, variation, and taxonomy of *Topaza* hummingbirds (Aves: Trochilidae). *Ornitologia Neotropical* 11:123–142.

Humphrey, P. S., and K. C. Parkes (1959). An approach to the study of molts and plumages. *The Auk* 76:1–31.

Hurly, T. A., R. D. Scott, and S. D. Healy (2001). The function of displays of male Rufous Hummingbirds. *The Condor* 103: 647–651.

Johnson, E. I., and J. D. Wolfe (2018). Molt in Neotropical birds: Life history and aging criteria. *Studies in Avian Biology* 51.

Kodric-Brown, A., and J. H. Brown (1978). Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant Rufous Hummingbirds. *Ecology* 59:285–296.

Lopez-Segoviano, G., R. Bribiesca, and M. Del Coro Arizmendi (2018). The role of size and dominance in the feeding behaviour of coexisting hummingbirds. *Ibis* 160. In press.

Lourenço, P. M., and T. Piersma (2015). Migration distance and breeding latitude correlate with the scheduling of prealternate body moult: A comparison among migratory waders. *Journal of Ornithology* 156:657–665.

McGuire, J. A., C. C. Witt, J. V. Remsen, Jr., A. Corl, D. L. Rabosky, D. L. Altshuler, and R. Dudley (2014). Molecular phylogenetics and the diversification of hummingbirds. *Current Biology* 24: 910–916.

Meadows, M. G., T. E. Roudybush, and K. J. McGraw (2012). Dietary protein level affects iridescent colorations in Anna's Hummingbirds, *Calypte anna*. *Journal of Experimental Biology* 215:2742–2750.

Oberholser, H. C. (1974). *The Bird Life of Texas*. University of Texas Press, Austin, TX, USA.

Phillips, A. R. (1975). The migrations of Allen's and other hummingbirds. *The Condor* 77:196–205.

- Prum, R. O., J. S. Berv, A. Dornburg, D. J. Field, J. P. Townsend, E. M. Lemmon, and A. R. Lemmon (2015). A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nature* 526:569–573.
- Pyle, P. (1997). Identification Guide to North American Birds, part 1. Slate Creek Press, Bolinas, CA, USA.
- Pyle, P. (1998). Eccentric first-year molts in certain tyrannid flycatchers. *Western Birds* 29:29–35.
- Pyle, P. (2005). Molts and plumages of ducks. *Waterbirds* 28:208–219.
- Pyle, P. (2007). Revision of molt and plumage terminology in ptarmigan (Phasianidae: *Lagopus* spp.) based on evolutionary considerations. *The Auk* 124:508–514.
- Pyle, P. (2008). Identification Guide to North American Birds, part 2. Slate Creek Press, Point Reyes Station, CA, USA.
- Pyle, P., and M. Reid (2016). Molts and plumages in the Long-tailed and other jaegers: An “alternate” explanation for nonbreeding plumages? *Western Birds* 47:242–257.
- Pyle, P., A. Engilis, Jr., and D. A. Kelt (2015). Manual for ageing and sexing the landbirds of Bosque Fray Jorge National Park and north-central Chile, with notes on range and breeding seasonality. The Occasional Papers of the Louisiana State University Museum of Natural Science, Special Publications. <http://www.museum.lsu.edu/occpap.html>
- Pyle, P., S. N. G. Howell, and G. M. Yanega (1997). Molt, retained flight feathers and age in North American hummingbirds. In *The Era of Allan Phillips: A Festschrift* (R. W. Dickerman, Editor). Horizon Communications, Albuquerque, NM, USA. pp. 155–166.
- Pyle, P., W. A. Leitner, L. Lozano-Angulo, F. Avilez-Teran, H. Swanson, E. G. Limón, and M. K. Chambers (2009). Temporal, spatial, and annual variation in the occurrence of molt-migrant passerines in the Mexican monsoon region. *The Condor* 111:583–590.
- Rohwer, S., L. K. Butler, and D. Froehlich (2005). Ecology and demography of east–west differences in molt scheduling of Neotropical migrant passerines. In *Birds of Two Worlds: The Ecology and Evolution of Migratory Birds* (R. Greenberg and P. P. Marra, Editors). Johns Hopkins University Press, Baltimore, MD, USA. pp. 87–105.
- Russell, R. W., F. L. Carpenter, M. A. Hixon, and D. C. Paton (1994). The impact of variation in stopover habitat quality on migrant Rufous Hummingbirds. *Conservation Biology* 8:483–490.
- Stiles, F. G. (1980). The annual cycle in a tropical wet forest hummingbird community. *Ibis* 122:322–343.
- Thompson, C. W., and M. Leu (1994). Determining homology of molts and plumages to address evolutionary questions: A rejoinder regarding emberizid finches. *The Condor* 96:769–782.
- Van Devender, T. R., W. A. Calder, K. Krebbs, A. L. Reina G., S. M. Russell, and R. O. Russell (2004). Hummingbird plants and potential nectar corridors for the Rufous Hummingbird in Sonora, Mexico. In *Conserving Migratory Pollinators and Nectar Corridors in Western North America* (G. P. Nabhan, R. C. Brusca, and L. Holter, Editors). University of Arizona Press, Tucson, AZ, USA. pp. 96–121.
- Weidensaul, S., T. R. Robinson, R. R. Sargent, and M. B. Sargent (2013). Ruby-throated Hummingbird (*Archilochus colubris*), version 2.0. In *Birds of North America* (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. <https://birdsna.org/Species-Account/bna/species/rthhum>
- Williamson, F. S. L. (1956). The molt and testis cycle of the Anna hummingbird. *The Condor* 58:342–366.
- Wright, J. R., C. M. Tonra, and L. L. Powell (2018). Shorebirds in disguise: Prealternate molt migration in a passerine bird. *The Condor* 120. In press.
- Zenzal, T. J., Jr., and F. R. Moore (2016). Stopover biology of Ruby-throated Hummingbirds (*Archilochus colubris*) during autumn migration. *The Auk: Ornithological Advances* 133: 237–250.
- Zimmer, J. T. (1950). *Studies of Peruvian birds* 56: The genera *Eutoxeres*, *Campylopterus*, *Eupetomena*, and *Florisuga*. *American Museum Novitates* 1450:1–14.