

## ANNUAL MOLT IN RUBY-THROATED AND BLACK-CHINNED HUMMINGBIRDS<sup>1</sup>

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**Abstract.** Details of the annual molt in Ruby-throated Hummingbirds (*Archilochus colubris*) and Black-chinned Hummingbirds (*Archilochus alexandri*) are presented. Young of both species hatch essentially naked but within three weeks acquire a full set of feathers. After the birds migrate to winter quarters, these feathers are replaced completely before the first year of age and annually thereafter. The postnuptial molt in adult males and females is similar within species and proceeds at about the same rate. The same is true for young birds in juvenal plumage, though molting is generally initiated and completed later than in adults. The period required for the molt of remiges and rectrices in an individual is estimated at around four months, while on a population basis it is underway for 7-8 months. Comparisons of the annual molt in Ruby-throated and Black-chinned Hummingbirds to other hummingbirds show that there are numerous similarities, differences being primarily attributable to migrant versus resident status.

**Key words:** Molt; plumage; Ruby-throated Hummingbird; Black-chinned Hummingbird; Archilochus; Trochilidae.

**Resumen.** La muda anual está detallada en el Chupaflor Garganta de Rubí (*Archilochus colubris*) y el Chupaflor Terciopelo Barbanegro (*Archilochus alexandri*). Jovenes de los dos especies empollan esencialmente nudos pero dentro de tres semanas adquieren un completo vestido de plumas. Después las aves migran a sus sitios invernales, estas plumas son repuestas completamente a dentro del año primero y anualmente después de eso. La muda de adultos es semejante en machos y hembras en cada especie y procede mas o menos en los mismos incrementos proporcionales. Esto también es verdad para los juveniles, aún ellos por lo general inician y completan la muda después de los adultos. La muda de las primarias y secundarias y plumas de la cola dura unos cuatro meses en aves individuales y 7-8 meses en poblaciones. Comparaciones en la muda entre estas y otras chupafloras muestran numerosos similitudes, y las diferencias son primariamente entre los especies que son residentes contra migratorios.

**Palabras claves:** Muda; plumaje; Chupaflor Garganta de Rubí; Chupaflor Terciopelo Barbanegro; Archilochus; Trochilidae.

### INTRODUCTION

Ruby-throated (*Archilochus colubris*) and Black-chinned (*Archilochus alexandri*) Hummingbirds are two of the most familiar and well-studied members of the Trochilidae in North America. Despite this, major gaps remain in our knowledge of their biology. This paper, which focuses on molt, is part of a concerted effort aimed at remedying omissions. The extended objective is to characterize both species as completely as possible so that their affinity to each other and to a number of other closely related species can be assessed (see Mayr and Short 1970).

Knowledge of molt and how it relates to the annual cycle is essential to an in-depth under-

standing of avian biology. Averaged over the entire molting period, energy expenditures required for molt are typically equal to 20-40% of the basal metabolic rate (Walsberg 1983), although data on this are lacking for hummingbirds. Given these estimates, molting is clearly energetically expensive and amounts to more energy than that required for the mere synthesis of keratin and concurrent increase in blood volume associated with the process (see King and Murphy 1990). Because of its energetic cost, birds schedule molt in a variety of ways in relation to other aspects of the annual cycle. Many birds, for example, have developed cycles in which molt, breeding, and migration occur with minimal overlap, thus avoiding undue energetic stress (e.g., Kendeigh 1949, Pitelka 1958, Farner 1964, Payne 1973, and Morton and Morton 1990).

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Hummingbirds is poorly understood, primarily because both species molt after migrating to wintering grounds, which historically have meant and mainly remain areas in Mexico for Black-chinned Hummingbirds and throughout much of Mexico and Central America for Ruby-throated Hummingbirds. Even so, for a group as diverse and popular as the Trochilidae, it is amazing that so little is known. Perhaps the most extensive work to date on species occurring in portions of North America and Mexico is that of Wagner (1955, 1957), who provided at least partial data for 20 species. For species primarily confined to South America, works by Ruschi (e.g., 1962a, 1962b, 1962c, and 1962d) are the most comprehensive. Beyond this, knowledge of molt in hummingbirds is found sporadically throughout the literature. Williamson (1956) provides an excellent account of molt in Anna's Hummingbird (*Calypte anna*), while Aldrich (1956) provides data on molt in Allen's (*Selasphorus sasin*) and Rufous (*Selasphorus rufus*) Hummingbirds. Data on the Long-tailed Hermit (*Phaethornis superciliosus*), a tropical species, is provided by Stiles and Wolf (1974). Stiles (1983) also has provided data on several species (primarily tropical) in the genus *Selasphorus*. Beyond this one must refer to works such as Bent (1940) and references cited there (e.g., Dickey and van Rossem 1938), Norris et al. (1957), and Leberman (1972) to glean additional information.

## MATERIALS AND METHODS

Primary and secondary flight feathers of the wing (remiges) and tail feathers (rectrices) are assigned numbers for the purpose of study. The primaries are numbered from the carpal joint (wrist) outward and number ten in hummingbirds. The secondary flight feathers are supported on the ulna and also begin with number one at the wrist and run inward along the forearm toward the body (one through six in hummingbirds). The innermost tail feathers of each half of the tail begin with number one and proceed outward through number five in hummingbirds.

I recorded the molt of Ruby-throated and Black-chinned Hummingbirds on diagrams similar to those developed by Wagner (1955). Diagrams were scored using a system similar to that employed by Pitelka (1958). The molt of the ten primaries and five rectrices (molt generally symmetrical between wings and left and right sides

of tail) was scored as follows: old/worn (0.0 pts.), missing (0.5 pts.), emerging (1.0 pts.), 25% emerged (1.5 pts.), 50% emerged (2.0 pts.), 75% emerged (2.5 pts.), and fully emerged/new (3.0 pts.) By this system, a bird having completed the molt of all ten primaries would score 30 points ( $3 \times 10$ ), whereas the completed molt of the rectrices would total 15 points ( $3 \times 5$ ).

The condition and molt of the secondaries was of interest because they are useful in assessing age (see below). Because it was often nearly impossible (without damaging the specimen) to tell which secondary was which (i.e., its position and number), the molt of secondaries was scored more simply by assigning 0.5 points to cases in which two or fewer secondaries were freshly molted or missing. A value of 1.0 point was assigned if there were more than two freshly molted secondaries. No points were assigned when all secondaries were old/worn.

The molting of primaries generally precedes that of the rectrices (onset of rectrix replacement begins as the last of the primaries are replaced). Composite scores are thus easily interpreted in that a bird midway through the molt would score approximately 23 points (bulk if not total score attributed to primary molt) and a completed molt of remiges and rectrices would total 46 points.

Birds were aged using a variety of techniques, most notably examination of the bill for corrugations (Ortiz-Crespo 1972), which are indicative of immaturity. With age, corrugations disappear and one must rely on other characters (see Baltosser 1987). Aging by bill corrugations is not infallible, particularly for birds that are 6–8 months of age. I therefore developed another set of criteria which, if used in conjunction with the former, enabled me to age nearly all birds as adults ( $> 1$  year) or subadults ( $> 1$  month and  $< 1$  year).

The characters to separate young and old birds developed for this study are based on the presence or absence of buff edging on the secondaries and edge of the primary coverts. Young birds, particularly females, have considerable buffy fringe that is often retained into January and February, after which these feathers are molted. This condition is not as evident in young males, but these can generally be aged by other characters (e.g., shape of inner primaries and/or presence of a few gorget feathers). Grouping birds into adult and subadult categories by these plumage characters is thus relatively straightforward.

TABLE 1. Progression of molt (remiges and rectrices) in Ruby-throated Hummingbirds as shown by average scores within seasonal groupings (completed molt scores 46).

Months	Adult females	Adult males	Subadult females	Subadult males
Sept./Oct.				
$\bar{x}$	1.37	0.86	0.14	0.02
SD	3.71	3.21	0.42	0.14
<i>n</i>	15	22	50	49
Nov./Dec.				
$\bar{x}$	16.50	—	5.85	5.77
SD	5.12	—	8.26	7.00
<i>n</i>	16	0	10	11
Jan./Feb.				
$\bar{x}$	28.42	23.80	22.17	16.56
SD	9.38	2.95	10.29	4.94
<i>n</i>	19	5	9	8
Mar./Apr.				
$\bar{x}$	42.36	45.42	28.83 <sup>1</sup>	41.75 <sup>2</sup>
SD	5.79	1.99	2.25	0.35
<i>n</i>	21	30	3	2

<sup>1</sup> Most young females indistinguishable from adult females by this time; these represent exceptions.

<sup>2</sup> Young males still distinguished by gorget and tail.

Adults can also possess fringed edges in fresh plumage, but these are more grayish than buffy in coloration.

The most informative data regarding the molt of remiges and rectrices in Ruby-throated and Black-chinned Hummingbirds comes from birds taken on wintering grounds. Birds examined from other periods are still useful in that they demonstrate: (1) the lack of molt, (2) the extent to which feathers are lost prematurely, and (3) the number of gorget feathers in place prior to full-scale molt of the chin and throat region of subadult males in late winter and spring.

My study of Ruby-throated Hummingbirds is based on 427 birds (196 adults and 231 young) taken from throughout the winter (much of central and southern Mexico south to Panama), summer (southern and southeastern Canada throughout the mid-west and eastern United States south to the gulf coast), and migratory (all points in between) ranges. Specimens were examined from Canada (1 bird), Belize (1), Costa Rica (15), Guatemala (9), Honduras (6), and Nicaragua (1) but most were taken on wintering grounds in Mexico or within the United States. Locations in Mexico include the states of Chiapas (15 birds), Coahuila (1), Colima (6), Guanajuato (4), Guerrero (32), Hidalgo (1), Jalisco

(7), México (7), Michoacán (14), Morelos (14), Nayarit (5), Nuevo León (2), Oaxaca (40), Puebla (1), San Luis Potosí (24), Sinaloa (3), Tabasco (1), Tamaulipas (9), Veracruz (23), Yucatán (11), and localities unknown ("Mexico" only location given = 4). From the United States, birds from Connecticut (1), Delaware (1), Georgia (9), Illinois (1), Indiana (3), Iowa (3), Kentucky (1), Louisiana (33), Maine (1), Massachusetts (2), Michigan (36), Mississippi (1), New Hampshire (1), New Mexico (2), New York (14), North Carolina (3), Ohio (1), Pennsylvania (3), Texas (28), Virginia (4), Washington D.C. (8), West Virginia (11), and Wisconsin (1) complete the list.

The Black-chinned Hummingbird findings are based on 611 birds (403 adults and 208 subadults) taken from throughout the winter (primarily Mexico but some records from the southern U.S.), summer (primarily the western U.S. but some from Mexico), and migratory (all points in between) ranges. Locations within Mexico include the states of Baja California Norte (3 birds), Coahuila (14), Chihuahua (16), Colima (7), Durango (10), Guanajuato (22), Jalisco (10), Michoacán (16), Morelos (1), Nayarit (1), Nuevo León (5), San Luis Potosí (25), Sinaloa (12), Sonora (14), and Tamaulipas (3). Birds examined from localities within the United States include Arizona (126), California (152), Colorado (2), Louisiana (3), New Mexico (98), Texas (69), Utah (1), and Washington (1).

## RESULTS AND DISCUSSION

### TIMING OF MOLT

The overall progression of molt in Ruby-throated Hummingbirds is shown in Table 1 and that of Black-chinned Hummingbirds in Table 2. The molt of remiges and rectrices in Black-chinned Hummingbirds is approximately one month ahead of Ruby-throated Hummingbirds, as many adult Black-chinned Hummingbirds score in the forties (completed molt scores 46) by February while Ruby-throated Hummingbirds take until March to achieve similar scores. In both species, molt in adults tends to precede that in subadults. In Ruby-throated Hummingbirds, for example, January scores for adults average 23.18, whereas subadult scores average 16.77. December scores for adult Black-chinned Hummingbirds average 32.19, while those of subadults for this period average 13.42. These comparisons show also that, at least through the first half of the molt, similar-

TABLE 2. Progression of molt (remiges and rectrices) in Black-chinned Hummingbirds as shown by average scores within seasonal groupings (completed molt scores 46).

Months	Adult females	Adult males	Subadult females	Subadult males
Sept./Oct.				
$\bar{x}$	10.10	6.28	0.00	0.00
SD	11.68	7.58	0.00	0.00
<i>n</i>	10	9	18	23
Nov./Dec.				
$\bar{x}$	31.64	31.25	10.58	15.63
SD	6.12	13.08	11.66	5.76
<i>n</i>	7	2	6	4
Jan./Feb.				
$\bar{x}$	42.50	36.94	19.50	15.31
SD	3.69	8.18	9.90	8.36
<i>n</i>	6	9	2	8
Mar./Apr.				
$\bar{x}$	45.53	46.00	— <sup>1</sup>	38.36 <sup>2</sup>
SD	1.02	0.00	—	6.48
<i>n</i>	18	30	0	7

<sup>1</sup> Most young females indistinguishable from adult females by this time.

<sup>2</sup> Young males still distinguished by gorget and tail.

aged males and females have molts that progress at approximately the same rate. Lack of data prohibits extension of this generalization to the remainder of the molt cycle, but available information suggests that they remain similar.

#### MOLT OF PRIMARIES

Data characterizing primary molt in Ruby-throated Hummingbirds are shown in Table 3. Relatively few adults begin this molt in September; most do so in October. Due to limited data, the initiation of primary molt by subadult Ruby-throated Hummingbirds is sketchy, as the data I have show no molt until November. By this time their molt has progressed to about one-third of that of adults (at least adult females). Comparisons for January, in which there are data for all age and sex categories, show that adult males and females are similar, as are subadults to each other. These same data show that the molting of primaries by subadults lags somewhat behind adults, as is the case for the remainder of the molt for which data are available.

Timing of primary molt in Black-chinned Hummingbirds is shown also in Table 3. Since adults have already begun to molt primaries by September, whereas no subadults show any signs of molt, adults exhibit considerable molt by Oc-

TABLE 3. Primary molt in Ruby-throated (upper score) and Black-chinned (lower score) Hummingbirds as shown by the average score for each month (completed molt scores 30).

Month	Adult females	Adult males	Subadult females	Subadult males
Sept.				
	0.25	0.17	0.00	0.04
	3.71	3.86	0.00	0.00
Oct.				
	2.64	1.50	0.00	0.00
	23.50	14.75	0.00	0.00 <sup>1</sup>
Nov.				
	14.17	—	4.00	3.19
	25.50 <sup>1</sup>	—	9.50	18.75
Dec.				
	16.06	—	10.17	7.50
	24.50	24.00	10.88	12.50
Jan.				
	21.14	22.50	16.17	14.70
	—	21.17	17.00	9.88
Feb.				
	24.92	21.00 <sup>1</sup>	19.50	16.00
	29.00	29.00	—	19.38
Mar.				
	27.22	29.83	22.83	28.25
	29.38	30.00	—	26.70
Apr.				
	29.71	29.28	—	—
	29.93	30.00	—	30.00

<sup>1</sup> Sample size = 1.

tober (data on subadults is limited). By December, a period for which I have data for all age and sex categories, molt scores of adult males and females are similar, as are those of subadult males and females. Once again, as was the case in Ruby-throated Hummingbirds, the molt in subadult birds lags behind adults, though in this case by as much as half (Table 3).

The sequence of primary molt is the same in both Ruby-throated and Black-chinned Hummingbirds. Molt proceeds from the inside out (i.e., beginning with primary 1), primaries being replaced sequentially through primary eight, after which primary ten is lost before number nine. Of the Ruby-throated Hummingbirds examined, 88% followed this sequence as did 94% of the Black-chinned Hummingbirds. A slight variation in this pattern resulted when two or more primaries from each wing were lost simultaneously, as opposed to the former case in which a second primary was not shed until the previous was at least well emerged from its sheath. This minor variation, which still followed the basic sequence, accounted for an additional 6% of all Ruby-throated Hummingbirds and all remaining Black-chinned Hummingbirds (i.e., 6%). Primary molt in the remaining Ruby-throated Hummingbirds (6%) can be described as erratic (i.e., there was no pattern among these remaining birds or similarity to the former sequences).

TABLE 4. Rectrix molt in Ruby-throated (upper score) and Black-chinned (lower score) Hummingbirds as shown by the average score for each month (completed molt scores 15).

Month	Adult females	Adult males	Subadult females	Subadult males
Sept.	0.00	0.00	0.17 <sup>2</sup>	0.00
	0.00	0.00	0.00	0.00
Oct.	0.00	0.20	0.10 <sup>3</sup>	0.00 <sup>4</sup>
	1.50 <sup>5</sup>	0.00	0.00	0.00 <sup>1</sup>
Nov.	1.17	—	0.00	1.88
	0.00 <sup>1</sup>	—	0.00	0.00
Dec.	1.36	—	0.00	0.17
	7.00	6.25	2.75	0.00
Jan.	1.21	1.13	1.42	0.70
	—	1.50	2.00	0.00
Feb.	6.46	0.00 <sup>1</sup>	11.17 <sup>6</sup>	2.00
	12.50	12.08	—	1.38
Mar.	12.54	14.79	5.17	13.50
	15.00	15.00	—	8.80
Apr.	15.00	15.00	—	—
	14.64	15.00	—	14.25

<sup>1</sup> Sample size = 1.

<sup>2</sup> No signs of molt in 22 of 26 birds (see text).

<sup>3</sup> No signs of molt in 20 of 24 birds (see text).

<sup>4</sup> Excluded 2 of 24 birds for premature molt (see text).

<sup>5</sup> Excluded 1 of 3 birds for premature molt (see text).

<sup>6</sup> Included, too late in season to automatically assign to premature loss.

#### MOLT OF RECTRICES

The progression of rectrix molt in Ruby-throated Hummingbirds is shown in Table 4. Tail feathers are more prone to loss than primaries when feathers are lost prematurely, e.g., narrowly escaping predation. For this reason, I have annotated the values presented in Table 4 for subadult females during September and for subadult females and males for October. In the latter case, 2 of 24 males were excluded because they had obviously lost their tails shortly after fledging. By October these two birds had replaced their tails with feathers that were similar if not the same as those of adult males (see Baltosser 1987 and Newfield 1992). Similarly, 22 of 26 subadult females in the September grouping showed no sign of molt, nor did 20 of the 24 for the month of October.

Molt of rectrices in Ruby-throated Hummingbirds does not begin in earnest until late January and early February, assuming the molt of birds of the same age is similar and that feathers have not been lost prematurely. By late March and early April, virtually all adult birds have completed this molt (completed rectrix molt = 15). Subadults are presumably not far behind, completing their molt by mid-to-late April.

The progression of rectrix molt in Black-

chinned Hummingbirds is shown also in Table 4. One adult female was omitted when I calculated the October average (1.50) for adult females because she had completed her molt (i.e., all feathers had been lost prematurely, as might occur in a near-fatal mishap). Molt in adults is well underway in many birds by December, and by late February several adults lack only one feather, completing this molt by mid-March. The data are incomplete for subadults but they tend to lag behind adults, undoubtedly completing the molt by mid-to-late April.

The rectrix molt is the same in both Ruby-throated and Black-chinned Hummingbirds. Feather loss and replacement proceeds from inside out (i.e., beginning with rectrix 1), with rectrices replaced in one of three sequences. In the first of these, which I deem to be typical (i.e., without premature loss), feather replacement progresses from the inside (rectrix 1) to the outside (rectrix 5). This was exhibited by 52% of the Ruby-throated Hummingbirds examined and 58% of all Black-chinned Hummingbirds. The second sequence, which accounts for 22% of all Ruby-throated and 19% of all Black-chinned Hummingbirds, is very similar to the first except that two or more feathers on each side of the tail are lost simultaneously, as opposed to the former in which a second rectrix was not shed until the previous feather had at least emerged from its sheath. The last category is undoubtedly influenced by premature losses, as there was no pattern among the remaining birds or similarity to the former sequences. The only item in common is the proportion of Ruby-throated (26%) and Black-chinned (23%) Hummingbirds in this category.

#### DURATION AND REPLACEMENT RATE

The extent of time required for individual Ruby-throated and Black-chinned Hummingbirds to molt primaries and rectrices, including estimated feather replacement rates, is presented in Table 5. Dates shown are for birds that have not lost feathers prematurely. Based on these data, the replacement rate is about one primary every two weeks for both species. However, molt proceeds rather rapidly through the first four or five primaries and then slows as the remaining feathers are shed and replaced, which is typical of many bird species (see Stresemann and Stresemann 1966). The replacement rate for rectrices, which are more prone to premature loss than remiges,

TABLE 5. Duration and replacement rate in the molt of primaries and rectrices in adult Ruby-throated and Black-chinned Hummingbirds.

Molt Species	Sex	Onset/Completion <sup>1</sup>	Duration (days)	Replacement rate <sup>2</sup>
<b>Primaries</b>				
Ruby-throated	F	25 Sept./07 Feb.	136	13.6 days
Ruby-throated	M	30 Sept./26 Feb.	150	15.0 days
Black-chinned	F	01 Aug./30 Dec.	152	15.2 days
Black-chinned	M	08 Sept./11 Feb.	157	15.7 days
<b>Rectrices</b>				
Ruby-throated	F	21 Nov./07 Feb.	79	15.8 days
Ruby-throated	M	29 Oct./04 Mar.	127	25.4 days
Black-chinned	F	22 Oct./26 Feb.	128	25.6 days
Black-chinned	M	05 Dec./18 Feb.	76	15.2 days

<sup>1</sup> Onset and completion as early as dates shown.

<sup>2</sup> Duration divided by number of primaries (10) or rectrices (5).

is again about the same for both species and averages three weeks per feather. Perhaps with more data (i.e., male Ruby-throated and female Black-chinned Hummingbirds), the replacement rate would be closer to one every two weeks as exhibited by female Ruby-throated and male Black-chinned Hummingbirds.

#### OTHER PLUMAGE

The molt of other features of the plumage in Ruby-throated and Black-chinned Hummingbirds frequently begins with the lower rump. If this occurs, then molt generally proceeds to the lower back, which in adults may begin by October. Molt then becomes rather general (a few feathers here and there), with this often well underway by January. Alternatively, birds may begin feather replacement through a general molt, as opposed to beginning with the rump and lower back. Either way, feather replacement tends to progress anteriorly, with the head molt (particularly around the base of the bill) the last to be completed. In adult males of both species, extensive molt of the head and chin (including gorget) occurs in early-to-mid-March. Feather replacement in the head region of adult females appears to follow the same sequence and is similar in its onset and completion.

The extent to which young male Ruby-throated and Black-chinned Hummingbirds acquire adult-type gorget feathers is variable. Males of both species generally, though not always (Baltosser 1987), have moderate to heavy streaking on the chin and usually possess at least one or two gorget feathers shortly after fledging. The major onset of feather replacement resulting in

a completed gorget does not take place (excluding premature loss, see Baltosser 1987 and Newfield 1992), however, until primaries have been replaced and the molt of rectrices has begun, which is not until late winter or early spring when birds are 8–10 months old.

Data on 112 young male Ruby-throated Hummingbirds taken between July and October show that 42 (37.5%) did not possess metallic gorget feathers. The remaining 70 (62.5%) had one or more gorget feathers; the median (data somewhat skewed) being 2.9 (mean = 3.8, SD = 3.4, range = 1–18). Similarly, 31 (17.0%) of 182 young male Black-chinned Hummingbirds (same seasonal period) did not possess black or metallic purple gorget feathers. The remaining 151 birds (83.0%) did have gorget feathers; the median being 2.2 (mean = 3.0, SD = 2.12, range = 1–10). In Ruby-throated Hummingbirds, young males on rare occasion may lack gorget feathers by late January, whereas the latest date for this in Black-chinned Hummingbirds is October.

Young males of either species add few gorget feathers during the period from November through February. The major onset of chin molt, which is best seen in males, does not take place until March. There are even a few birds that do not begin to molt in earnest until late March or even early April. Interestingly, adult males of both species tend to complete their gorgets one or two weeks earlier than many young males. Adult male Ruby-throated Hummingbirds have generally completed the molt of their gorgets by late March or early April. The data for adult male Black-chinned Hummingbirds indicate similar timing, though perhaps slightly more protracted

as indicated by the presence of a few pin feathers at the base of the bill in early-to-mid-May. The gorgets of many young male Ruby-throated Hummingbirds (contrary to Dickey and van Rossem 1938) and most Black-chinned Hummingbirds are not completed before April. Occasionally, young male Ruby-throated Hummingbirds may still be molting into late April and young male Black-chinned Hummingbirds into early May.

#### SUMMARY AND CONCLUSIONS

The timing, sequence, and many other aspects of molt in Ruby-throated Hummingbirds and Black-chinned Hummingbirds are similar. The principal details of molt in both species are as follows:

1. Ruby-throated and Black-chinned Hummingbirds migrate to winter quarters in worn plumage and then undergo a complete annual molt.

2. Young in juvenal plumage start replacing their flight feathers (barring premature loss) as early as November and acquire their first basic plumage by mid-April to early May (see Humphrey and Parkes 1959 for molt terminology).

3. Molt in Ruby-throated Hummingbirds is similar to that of Black-chinned Hummingbirds, except that in the Black-chinned it is often initiated earlier in the season.

4. Molt in adult males and females is similar and proceeds at about the same rate, as it does in young males and females. Adults, however, initiate and generally complete their molt before young birds.

5. On a population basis, the period over which molt is underway is 7–8 months. The period required for the molt of remiges and rectrices in an individual is estimated at around four months.

6. Loss and replacement of corresponding flight and tail feathers on both sides of the body occurs symmetrically.

7. Molting of the flight feathers begins with the primaries.

8. Molting of rectrices generally begins as the last of the primaries are replaced.

9. Loss and replacement of contour feathers is often variable; in some birds it begins with the lower back and rump, whereas in other birds it begins with a more generalized molt. In either case, molt proceeds anteriorly, with the head region the last to be molted.

Details of molt in the family Trochilidae are

scant for a family of birds that contains well over 300 species. Birds hatch essentially naked, but within 21–22 days Ruby-throated and Black-chinned Hummingbirds acquire a complete set of feathers that are replaced completely prior to the first year of age and annually thereafter. The molt in both species is similar in many ways to that of other species (e.g., see Wagner 1955, 1957 and Tyrrell and Tyrrell 1985), though some of the details may differ. For example, molting and breeding show more overlap in Anna's Hummingbirds (Williamson 1956) and there is no consistent temporal relationship between timing of molt and breeding in Long-tailed Hermits (Stiles and Wolf 1974). Differences are perhaps largely attributable to the resident status of both species and to the timing of reproduction (nesting begins during winter months in Anna's and nesting in Long-tailed Hermits is opportunistic and dependent on local habitat conditions).

Once Ruby-throated and Black-chinned Hummingbirds arrive on their wintering grounds, molting occurs over a rather extended period (presumably an adaptation that conserves energy). Because hummingbirds are totally dependent upon flight, the loss of the outer primary (#10) before #9 may be critical, since #10 is the largest and occupies such a crucial position. The nonsequential molt pattern of the ninth and tenth primaries in hummingbirds is perhaps an adaptation to minimize the loss of surface area and thus maintain the integrity of the wing disc during molt (see Epting 1980). In all other respects, the molting of primaries in hummingbirds is similar to many bird species in that molt proceeds sequentially from the inside out.

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#### LITERATURE CITED

- ALDRICH, E. C. 1956. Pterylography and molt of the Allen Hummingbird. *Condor* 58:121-133.
- BALTOSSER, W. H. 1987. Age, species, and sex determination of four North American hummingbirds. *N. Am. Bird Bander* 12:151-166.
- BENT, A. C. 1940. Life histories of North American cuckoos, goatsuckers, hummingbirds, and their allies [part two]. Dover Publications, New York.
- DICKEY, D. R., AND A. J. VAN ROSSEM. 1938. The birds of El Salvador. Field Museum of Natural History Publ. Zool., Vol. 23. Chicago.
- EPTING, R. J. 1980. Functional dependence of the power for hovering on wing disc loading in hummingbirds. *Physiol. Zool.* 53:347-357.
- FARNER, D. S. 1964. The photoperiodic control of reproductive cycles in birds. *Am. Sci.* 52:137-156.
- HUMPHREY, P. S., AND K. C. PARKES. 1959. An approach to the study of molts and plumages. *Auk* 76:1-31.
- KENDEIGH, S. C. 1949. Effect of temperature and season on the energy resources of the English Sparrow. *Auk* 66:113-127.
- KING, J. R., AND M. E. MURPHY. 1990. Estimates of the mass of structures other than plumage produced during molt by White-crowned Sparrows. *Condor* 92:839-843.
- LEBERMAN, R. C. 1972. Identify, sex, and age it: Key to age and sex determination of Ruby-throated Hummingbirds in autumn. *Inland Bird Banding News* 44:197-202.
- MAYR, E., AND L. L. SHORT, JR. 1970. Species taxa of North American birds: A contribution to comparative systematics, p. 1-127. *In* R. A. Paynter [ed.], *Publ. Nuttall Ornithol. Club*, No. 9. Cambridge, MA.
- MORTON, G. A., AND M. L. MORTON. 1990. Dynamics of postnuptial molt in free-living Mountain White-crowned Sparrows. *Condor* 92:813-828.
- NEWFIELD, N. L. 1992. Louisiana's hummingbirds. Louisiana Department of Wildlife and Fisheries, Bourque Printing Co., Baton Rouge, LA.
- NORRIS, R. A., C. E. CONNELL, AND D. W. JOHNSTON. 1957. Notes on fall plumages, weights, and fat condition in the Ruby-throated Hummingbird. *Wilson Bull.* 69:155-163.
- ORTIZ-CRESPO, F. I. 1972. A new method to separate immature and adult hummingbirds. *Auk* 89:851-857.
- PAYNE, R. B. 1973. Mechanisms and control of molt, p. 104-157. *In* D. S. Farner and J. R. King [eds.], *Avian biology*, vol. 2. Academic Press, New York.
- PITELKA, F. A. 1958. Timing of molt in Steller Jays of the Queen Charlotte Islands, British Columbia. *Condor* 60:38-49.
- RUSCHI, A. 1962a. A muda em: *Heliomaster furcifer* (Shaw) e *Heliomaster squamosus* (Temminck). (Aves, Trochilidae). *Bol. Mus. Biol. Prof. Mello-Leitão* 35:1-2.
- RUSCHI, A. 1962b. A muda em: *Calliphlox amethystina* (Boddaert) e *Calliphlox mitchelli* (Bourcier). (Aves, Trochilidae). *Bol. Mus. Biol. Prof. Mello-Leitão* 36:1-2.
- RUSCHI, A. 1962c. A muda em: *Chrysolampis mosquito* (Linne) e *Chlorestes notatus notatus* (C. Reichembach). (Aves, Trochilidae). *Bol. Mus. Biol. Prof. Mello-Leitão* 37:1-2.
- RUSCHI, A. 1962d. A muda nos Trochilidae. *Bol. Mus. Biol. Prof. Mello-Leitão* 38:1-16.
- STILES, F. G. 1983. Systematics of the southern forms of *Selasphorus* (Trochilidae). *Auk* 100:311-325.
- STILES, F. G., AND L. L. WOLF. 1974. A possible circannual molt rhythm in a tropical hummingbird. *Am. Nat.* 108:341-354.
- STRESEMANN, E., AND V. STRESEMANN. 1966. Die Mauser der Vögel. *J. Ornithol.* 107:1-447.
- TYRRELL, E. Q., AND R. A. TYRRELL. 1985. Hummingbirds, their life and behavior. Crown Publ., New York.
- WAGNER, H. O. 1955. The molt of hummingbirds. *Auk* 72:286-291.
- WAGNER, H. O. 1957. The molting periods of Mexican hummingbirds. *Auk* 74:251-257.
- WALSBERG, G. E. 1983. Avian ecological energetics, p. 161-220. *In* D. S. Farner, J. R. King, and K. C. Parkes [eds.], *Avian biology*, vol. 7. Academic Press, New York.
- WILLIAMSON, F.S.L. 1956. The molt and testis cycle of the male Anna Hummingbird. *Condor* 58:342-366.