

MOLT, RETAINED FLIGHT FEATHERS AND AGE IN NORTH AMERICAN HUMMINGBIRDS

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ABSTRACT.—We examined specimens to document the timing, sequence, extent and location of prebasic molts in eight species of North American hummingbirds. Feather replacement sequence and duration in seven migratory species is similar to that documented for the Anna's Hummingbird (*Calypte anna*) by Williamson (1956). The molt of Costa's Hummingbird (*Calypte costa*) differs from that of six other migratory species in occurring during the summer and fall rather than during the winter and spring. Significant differences in timing were found between the first and adult prebasic molts of most species; however, little relationship was found between timing and sex, or duration and either age or sex. Retained flight feathers, especially rectrices and secondaries, were found in a very small proportion (1.0%) of hummingbirds among five species; incomplete gorgets were found in 10.3% of males of all species; and a juvenal characteristic, white in the outermost rectrices, was found in 5.4% of males among five species. We propose that most hummingbirds with these retained juvenal feathers and/or characteristics can be reliably aged as second-year birds. The scattered iridescent feathers acquired by first-year males may be part of a "presupplemental" molt, as these appear to be fully replaced for a second time at the end of what we consider the first prebasic molt. Our results reveal the need for further investigation of several interesting aspects of hummingbird molt in relation to annual cycles.

INTRODUCTION

As in other terrestrial non-passerines (Pyle 1995), the sequence, extent, and timing of molt in hummingbirds has received little attention. Exceptions to this, and to the study of molt in general (see Thompson and Leu 1994), are the excellent studies on Allen's (*Selasphorus sasin*) and Anna's (*Calypte anna*) hummingbirds published in 1956 by colleagues E.C. Aldrich and F.S.L. Williamson, respectively. Williamson chose Anna's for his analysis because it is the only resident hummingbird species in North America (north of Mexico; excepting the local race of the Allen's Hummingbird, *S.s. sedentarius*), allowing the entire molt cycle to be studied based on locally-collected specimens. All other North American hummingbirds are migratory, molting primarily on the non-breeding (hereafter "winter") grounds in Mexico and/or Central America (Bent 1940, Aldrich 1956, Williamson 1956, Ortiz-Crespo 1971, Stiles 1972, Phillips 1975, Baltosser 1994). The lack of adequate specimen material from these wintering areas has precluded further published analyses of molt in these species. Indeed, even Aldrich's (1956) study, primarily on the pterylography of Allen's Hummingbird, was limited to inferences on subsequent feather replacement due to lack of winter specimens. Except in Anna's Hummingbird, therefore, only minimal, scattered information has been published on the specifics of molt in North American species (e.g., Dickey and van Rossem 1938; Wagner 1948, 1955, 1957; Ortiz-Crespo 1971; Phillips 1975; Calder and Calder 1992; Calder 1993). [Since our study was completed, an independent investigation of molt in the two *Archilochus* species (Baltosser 1995) has also been published.] Some of these references infer that molts occur at different times in males and females but there have been no published data that critically examine sex-specific differences in timing.

Most authors have generally assumed that both the first and the adult prebasic molts of hummingbirds are complete (Stone 1896, Forbush 1927, Bent 1940, Williamson

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and beyond their second year. See Pyle (1995) for more on age codes. We follow Humphrey and Parkes (1959) and Thompson & Leu (1994) for terminology on molts and plumages, except that we use the term "adult" in place of their "definitive" for molts and plumages of birds at least a year old. Primaries (p1-p10) and rectrices (r1-r5) were numbered distally (outward or away from the body) and secondaries (s1-s6) proximally (inward or toward the body).

On each specimen the plumage and flight feathers (here defined as the primaries, primary coverts, secondaries, and rectrices) were carefully studied for evidence of active molt, incomplete replacement of flight or gorget feathers, and/or retention of juvenal characteristics in adult feathers. Progression of active molt on each specimen was scored according to the primaries, 0-10, indicating the number of primaries that had been fully-replaced. Birds collected subsequent to each species' breeding season that had not started molting were scored 0 and pre-breeding birds that had completed molting were scored 10. For each species a molting period was somewhat arbitrarily defined as from 20 days before until 20 days after the first and last observation of active primary molt, respectively. Predicted mean dates for commencement, completion and thus duration of primary molt were calculated with Type 2 (within molting periods) and Type 3 models presented by Underhill and Zucchini (1988). These were compared with results of simple linear regression on birds in molt using date as the dependent variable (FIG 1; see Pimm 1978, Underhill and Zucchini 1988). All statistical analyses were performed using the STATA statistics program (Computing Resource Center 1992).

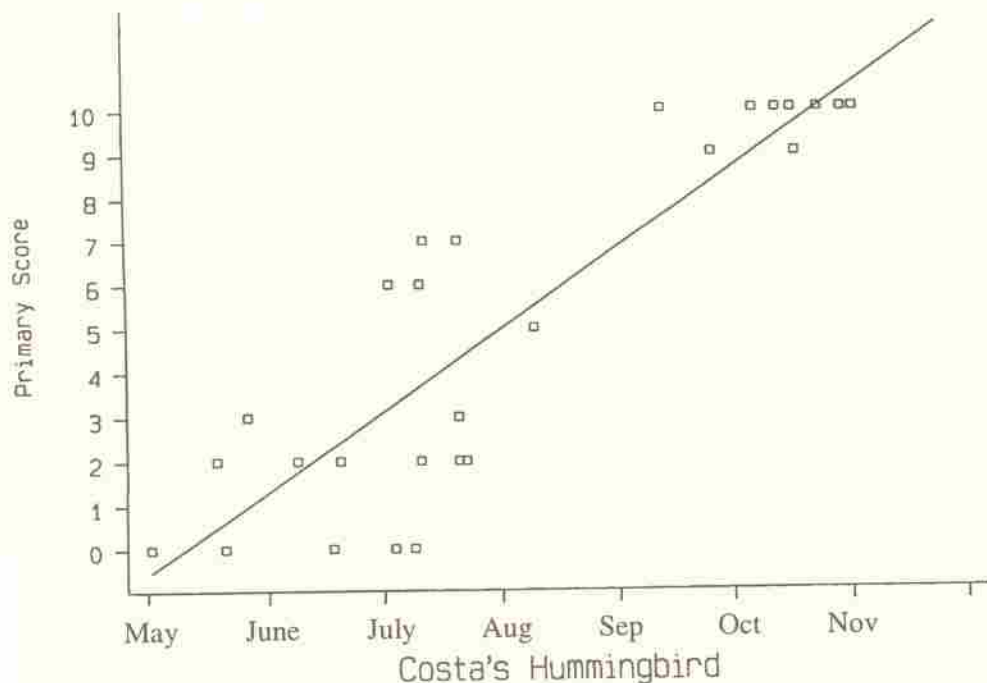


FIG 1. Timing of primary molt in Costa's Hummingbird. The linear regression line was fitted using primary score (on actively molting birds only) rather than date as the dependent variable, thus, the line estimates commencement of primary molt in the earliest bird to completion in the latest, or overall duration, rather than primary molt of the "average" individual (see Pimm 1978).

TABLE 1
OBSERVED¹ AND PREDICTED MEAN² TIMING AND DURATION OF MOLTS IN
MIGRATORY NORTH AMERICAN HUMMINGBIRDS, COLLECTED DURING MOLTING PERIODS (SEE TEXT).

Species	N	Observed			Predicted Mean		
		First Date	Last Date	Days Duration	First Date	Last Date	Days Duration
Ruby-throated	46	31 Oct	7 Apr	158	26 Oct	13 Mar	139
Black-chinned	20	1 Sep	22 Feb	174	11 Sep	20 Feb	162
Costa's	28	2 Jun	1 Nov	152	12 Jun	21 Oct	131
Calliope	16	14 Sep	15 Apr	213	30 Aug	31 Mar	212
Broad-tailed	24	8 Oct	10 Mar	153	11 Oct	1 Mar	141
Rufous	58	1 Sep	6 Mar	186	24 Sep	28 Jan	126
Allen's	13	20 Aug	12 Jan	145	22 Aug	8 Dec	118

¹ Observed dates are the first and last date a specimen was recorded with molting primaries.

² Predicted mean dates for the populations were calculated with Type 2 models presented by Underhill and Zucchini (1988; see text), on all birds within our defined molting periods.

RESULTS AND DISCUSSION

Molt in migratory hummingbirds.—Examination of 205 specimens collected during molting periods indicate that the sequence of molt in all migratory North American hummingbirds is similar to that of Anna's Hummingbird (Williamson 1956; see also Humphrey and Parkes 1959). Flight-feather molt begins with the first one to four primaries (among p1-p4). Primary replacement proceeds distally, and about the time that p6 is dropped the secondaries begin to molt both distally and proximally from the outsides. Specimen examination indicated that the sequence of secondary replacement typically is s1-s6-s2-s5-s3-s4, although a few specimens appeared to have one or two pairs of these feathers switched in order. Primary coverts are typically replaced with their corresponding primaries. Replacement of rectrices also begins about the time that p6 is dropped and usually proceeds distally, from the center (r1) to the lateral (r5) feathers, although in some specimens there was evidence that the outer rectrix (r5) could be replaced before the adjacent one (r4) or two (r3-r4) feathers. The outer primaries are replaced in order p7-p8-p10-p9 (see Wagner 1955, Williamson 1956). The gorget feathers of the male are the last to be renewed, replacement occurring rapidly and beginning sometime after the primary molt is complete.

An unexpected finding of this study is that Costa's Hummingbird exhibits an entirely different molt timing strategy from the other migratory species, molting in summer and fall (Fig. 1) as opposed to winter and spring (Table 1). This has not previously been reported and is contrary to indications in Bent (1940) that molt in this species occurs in winter and early spring. Costa's Hummingbird is generally considered a migratory species (e.g., American Ornithologist's Union 1983). It can be resident in certain areas, however, and is found regularly north to central California and Nevada during summer and fall, although most appear to withdraw to Mexico during the molting season (Baltosser 1989). All molting specimens examined by us had been collected in southern Arizona, southern California or Mexico. Perhaps the summer molt, as is also found in Anna's Hummingbird, represents an ancestral trait of the genus *Calypte*, despite the fact that most

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breeding of Costa's, at least north of Mexico, occurs later in the spring than in Anna's (Pitelka 1951, Williamson 1956, Baltosser 1989). The timing of molt in Costa's vs. the other North American hummingbirds, in consideration of breeding, migration and environmental cycles (see Stiles 1973), would be an interesting topic for further study.

The winter molt of the other six species showed some variation in timing (Table 1), as likely determined by differences in breeding season, food resources, and migratory strategies. The fact that Black-chinned molts 30-50 days earlier than Ruby-throated Hummingbird (see also Baltosser 1995) may assist in the difficult field identification of female *Archilochus* on the winter grounds. According to our data, Allen's Hummingbird molts 30-40 days before Rufous, less than the 2-3 months that the timing of both breeding and migration between these two species differ (Phillips 1975). It is possible that early breeding in Allen's Hummingbird represents a recent change in this species' evolutionary history, and that the timing of molt has evolved more slowly. Thus, in comparison with the biological cycle of Rufous Hummingbird, molt in Allen's is not as early and is quicker in duration (Table 1). More study is needed on the relationships of molt, migration, and winter food resources in migratory North American hummingbirds.

Prebasic molts in the species examined are protracted as in Anna's Hummingbird (Williamson 1956). Predicted mean duration of primary molt ranged from 118 days in Allen's Hummingbird to 212 days in Calliope Hummingbird (Table 1) with a mean among the seven migratory species of 143 days. These estimates tended to be longer than the 2.5 to 5 month (76-152 day) range that Williamson (1956) estimated for the duration of molt in individual Anna's Hummingbirds, and the 100-130 day period documented for a resident tropical species, Long-tailed Hermit (*Phaethornis superciliosus*; Stiles and Wolf 1974). On the other hand, the overall periods in which molting birds were observed (Table 1; range 145-213 days, mean 169 days) were generally shorter than both the eight-month period found in Anna's and the year-round molting of *Phaethornis*. Migratory species of birds typically show less variability in molt period than resident or semi-resident species because of the time and energy constraints of migration (Newton 1968, Baggott 1970, Jenni and Winkler 1994). The large difference between observed and predicted duration in Rufous Hummingbird (Table 1) may indicate a greater degree of individual variation in timing within this species.

Age-specific differences in the timing and duration of molt were found during this study in most species. These were statistically most pronounced in Ruby-throated and Rufous hummingbirds, due in part to larger sample sizes in these species (FIG 2). Statistically adjusting for primary molt score, AHY/ASYs molted earlier than HY/SYs in all species, significantly so (multiple ANOVA, $F > 5.9$, $P < 0.028$) in all except Calliope Hummingbird ($F = 2.86$, $P = 0.114$). Sex differences were not nearly as marked (FIG 2). Females molted slightly earlier than males in most species; however, this difference was only significant in Costa's Hummingbird ($F = 4.30$, $P = 0.049$); with greater samples it might also have become significant in Ruby-throated as well (see FIG 2). That age was a stronger influence than sex on timing was confirmed with multiple ANOVA including both age and sex as covariables: again, all but Calliope showed significant age-specific differences while no species showed significant sex-specific differences. Finally, when the entire sample was included (adjusting additionally for species), timing was significantly earlier in AHY/ASYs than in HY/SYs ($F(1,187) = 51.13$, $P < 0.001$) but was not significantly different in females vs. males ($F(1,187) = 0.57$, $P = 0.452$). Similar results were independently found in the two *Archilochus* species by Baltosser (1995).

Differences between age and sex classes in duration of molt were estimated by comparing slopes of linear regressions (see Fig. 2) with covariate analysis. No significant differences were found in duration of molt with either age or sex in any species or in all combined (interaction terms; $t < 1.64$, $P > 0.141$).

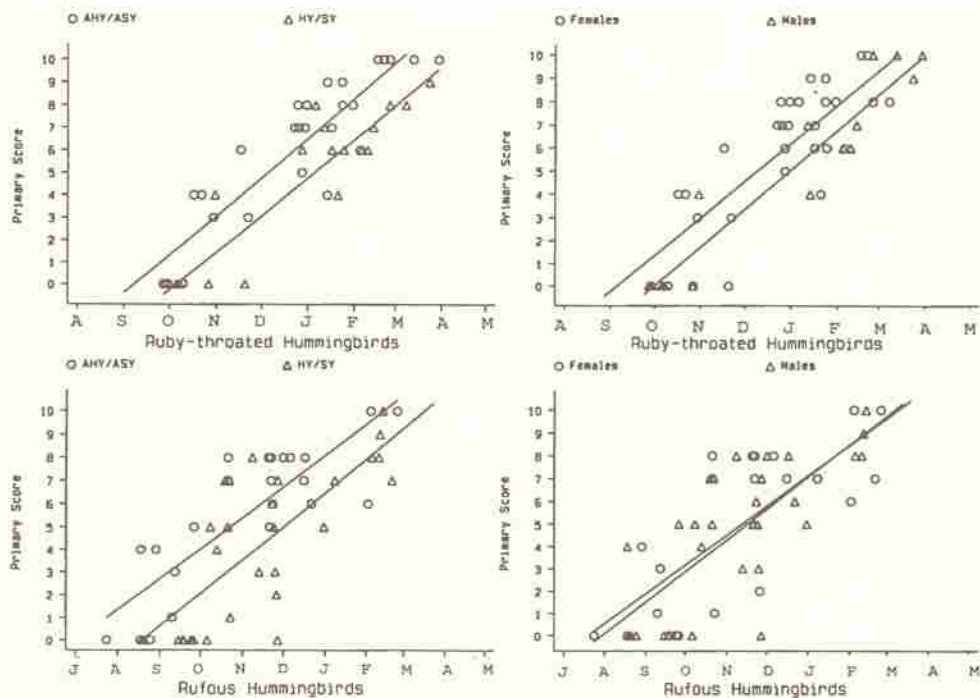


FIG 2. Variation by age and sex in timing of primary molt in Ruby-throated and Rufous hummingbirds. See Figure 1 regarding the regression lines. Age-specific differences were significant in both species $F(1,42)=13.7$, $P=0.001$, and $F(1,54)=6.43$, $P=0.014$, respectively), but sex-specific differences were not in either species ($F=3.40$, $P=0.072$ and $F=0.10$, $P=0.750$).

Several previous reports have assumed that hummingbirds of one sex molted before the other. While this may or may not be true in resident species or populations (Wagner 1948, 1955, 1957; Williamson 1956; Calder 1993), our data suggest that it is not the case in migratory North American populations. The lack of sex-specific differences in the duration of primary molts supports Williamson's (1956) suggestion that perceived differences are due mostly to the appended gorget molt of male hummingbirds, not found in females. The difference we found in molting by age in hummingbirds has not been previously emphasized, although Williamson's data generally indicated that AHY Anna's Hummingbirds molted before HYS. First prebasic molts are often later than adult prebasic molts in migratory birds (e.g., see Pyle et al. 1987), in part because it takes longer for 1st-year birds than adults to reach the winter grounds, and because first-year birds are generally less proficient at meeting the energy demands of molting (Jenni and Winkler 1994 and references therein).

Retained feathers and ageing AHY hummingbirds.—The examination of 1397 AHY specimens during the non-molting periods indicated that retained flight feathers are rare in hummingbirds (Table 2). Higher proportions of females with retained rectrices were encountered, while retained primaries, secondaries and rectrices in males occurred occasionally (Table 3). As in other birds with incomplete molts (Pyle 1995), retained feathers resulted from the arresting of the normal sequence, and thus included p8-p10, s3-s4, and r3-r5 (Table 3). The only feathers that could confidently be aged were the broad and rounded juvenal rectrices with distinct white tips retained by males (see Fig. 3); no retained adult rectrices were found. Although Williamson (1956) and Baltosser (1987)

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pointed out slight age-related differences in the shapes of the primaries and secondaries of both sexes, and the outer rectrices of females, we found that these differences could not be used to determine whether retained feathers were juvenal or adult, due to excessive wear of these feathers. Most birds of both sexes with retained flight feathers, however, could be aged SY by characteristics of rectrices and/or incomplete gorgets in males (see below; Table 3), and bill-corrugations in both sexes (Yanega et al., in review). We conclude that retained feathers probably occur rarely but regularly in SY/TYs but not normally in ASY/ATYs, as would be expected based on the later timing of molt in HY/SYs (see above).

We also found that occasional males of most species (e.g., Black-chinned Hummingbirds CAS45979 and MVZ101963, Anna's CAS35178, Costa's MVZ3654, Calliope CAS39465 and MVZ160566) and many male Broad-tailed hummingbirds (see also Calder and Calder 1992) retained a juvenal characteristic, white in the distal portions of the outer one or two rectrices, on otherwise adult-like rectrices (Table 2, Fig. 3). Except in Broad-tailed Hummingbird most (and probably all) males having adult rectrices with white were SYs by bill and/or gorget characteristics and, again, we propose that these birds are reliably aged HY/SY (*Calypte*) or SY/TY (*Archilochus*, *Stellula*) through the 2nd prebasic molt. In Broad-tailed Hummingbird, confirmed SYs averaged more white than birds that could only be aged AHY (Fig. 3), and we suspect that some birds might reliably be aged both SY/TY or, in the case of those that completely lack white in the outer rectrices, ASY/ATY. Caution is advised, however, as there also appeared to be a geographic difference in this character, birds from northern populations averaging more white than those of southern populations. More study on captive or recaptured, known-aged Broad-tailed Hummingbirds is needed to confirm the reliability of white in the rectrices as an ageing criterion at different latitudes. It is possible that male Broad-tailed and Calliope hummingbirds showed higher percentages of birds with white in the feathers due to the relatively larger outer rectrices in these species than in the other species examined. Unique patterns

TABLE 2
NUMBER OF BIRDS WITH RETAINED FLIGHT-FEATHERS, JUVENAL CHARACTERISTICS, AND/OR INCOMPLETE GORGETS IN NORTH AMERICAN HUMMINGBIRDS.

Species	N		Retained Flight-feathers		Incomplete Gorgets	White in Adult Rectrices
	Females	Males	Females	Males	Males	Males
Ruby-throated	21	26	1	0	2	0
Black-chinned	66	110	0	0	9	3
Anna's	129	216	4	2	30	2
Costa's	74	120	0	0	24	1
Calliope	82	117	1	0	8	11
Broad-tailed	40	78	4	0	7	29
Rufous	71	120	0	2	6	0
Allen's	54	70	0	0	3	0
TOTAL	537	860	10	4	89	46

Data are based on definitive-plumaged birds during non-molting periods (see text). Some retained flight-feathers in females and incomplete gorgets in males may have been overlooked due to the difficulty of inferring these conditions in very worn or ill-prepared specimens. See Table 3 for specifics of retained flight-feathers.

TABLE 3
HUMMINGBIRDS FOUND WITH RETAINED FLIGHT-FEATHERS

Species	Specimen	Sex	Age	Retained Feathers
Ruby-throated	CAS45975	F	SY	r3-r5
Anna's	CAS46025	F	SY	r5
Anna's	MVZ14597	F	SY	left r4-r5
Anna's	MVZ82222	F	SY	left r4
Anna's	MVZ11823	F	AHY	all rects
Anna's	CAS17721	M	SY	s4
Anna's	CAS46017	M	AHY	p9-p10, s3-s4, left r5
Calliope	CAS46108	F	AHY	r5
Broad-tailed	CAS75804	F	AHY	r5
Broad-tailed	MVZ162399	F	SY	left r5
Broad-tailed	MVZ150273	F	SY	right r3-r5
Broad-tailed	MVZ101998	F	SY	right r2-r5 ¹
Rufous	CAS46060	M	SY	p8-p10, s3-s4, r3-r4
Rufous	CAS42995	M	SY	p9-p10, s3-s4, r3-r5

¹ These were the only rectrices remaining on this bird.

Hummingbirds found with retained flight-feathers. Age was determined from factors other than those presented, i.e., incomplete gorgets on all four listed males and corrugations on the bill, the latter usually reliable for SYs (but not ASYs) until 1-2 months after the first prebasic molt (Yanega et al. in review). Unless specified, retained feathers were found symmetrically on both wings or sides of the tail. All birds with retained primaries had also retained corresponding primary coverts. See Table 2 for sample sizes of adults examined.

and shapes, intermediate between those of juvenal and adult rectrices, have also been noted in 1st-basic feathers of other species with large outer rectrices such as Lucifer Hummingbird (*Calothorax lucifer*; Wagner 1946; Pyle, specimen examination) and Slender Sheartail (*C. enicura*), Sparkling-tailed Woodstar (*Tilmatura dupontii*), and, possibly, *Chlorostilbon* emeralds (Howell and Webb 1995, Howell pers. obs.).

Incomplete "gorgets" (here including iridescent crown feathers) in males were found in all eight hummingbird species (Table 2). Incomplete gorgets took three forms. A very few males (e.g. Ruby-throated Hummingbird CAS35201 and Black-chinned Hummingbird CAS56343) had apparently retained one or two dull iridescent feathers from a previous feather generation. One Costa's (MVZ55222), five Rufous (e.g. CAS46060 and MVZ32984; see also Aldrich 1956, who mentions these individuals) and one Allen's Hummingbird (MVZ162354) had replaced all or most flight feathers (see Table 2), but had completely retained juvenal-plumaged gorgets, with only a few iridescent feathers. Most males with incomplete gorgets (89.9%) however, apparently had replaced the entire gorget but had retained juvenal characteristics in some 1st-basic feathers (Fig. 4). In the throats, these "incomplete gorgets" were often expressed by smaller iridescent tips to each feather, particularly those of the laterally-elongated feathers at the sides (Fig. 4B). In Anna's and Costa's hummingbirds many males had green feathers mixed in with the iridescent feathers of the crown (Fig. 4D). The higher incidence of incomplete crown feathering in *Calypte* than incomplete throat gorgets in the other species might result because the prebasic molt occurs at a younger age in these two species, especially in Costa's Hummingbird (see above). Interestingly, however, white in adult rectrices, which might also be expected to

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result from molt in younger birds, was relatively rare in *Calypte* (Table 2). Again, many birds with incomplete gorgets could be aged SY by bill characteristics and we are confident that incomplete gorgets are reliable indicators of HY/SY (*Calypte*) or SY/TY birds (see Aldrich 1956, Stiles 1973). Birds with complete gorgets, however, were not necessarily AHY/ASYs (*Calypte*) or ASY/ATYs. When ageing, beware that AHY/ASYs during molting periods (Table 1) can appear to have incomplete gorgets when in fact the iridescent feathers are just worn or in molt.

It is interesting that the iridescent gorget feathers which are apparently acquired slowly by HY/SY males during their first year (Aldrich 1956; Williamson 1956; Leberman 1967; Stiles 1972; Baltosser 1987, 1994) are typically replaced for a second time with the rest of the gorget feathers during the first prebasic molt. This was confirmed in our study by the near-complete lack of adult male specimens with contrastingly-tarnished gorget feathers, resembling in color and location those of HY/SYs in the period just preceding the molt. Also, two December HY (by bill corrugations) male specimens of Anna's Hummingbird (CAS45945 and CAS45948) were collected during complete molt of the throat, which included areas where previous iridescent feathers had undoubtedly been present. The replacement of these feathers during the first year thus might be considered part of a presupplemental molt (Thompson and Leu 1994), although the apparent gradual renewal of throat feathers is unlike that of other such molts. Perhaps a new molt term is needed, although the subject of molt already is overburdened with terminology.

CONCLUSIONS

In addition to documenting the timing of molts in migratory North American hummingbirds, previously undescribed in most species, our findings can be used to accurately age hummingbirds, including in some cases those in 1st-basic plumage. Specifically, males with retained juvenal rectrices, some (or much) in Broad-tailed Hummingbird white in 1st-basic outer rectrices (Fig. 3), and/or incomplete gorgets (Fig. 4) can be reliably aged HY/SY (*Calypte*; November-October) or SY/TY (*Archilochus*, *Stellula*, *Selasphorus*; April-March) through the 2nd prebasic molt. With more study, males of some species may be found to be reliably aged AHY/ASY by complete iridescent crowns (Anna's and Costa's) or ASY/ATY by entirely dark rectrices (Broad-tailed Hummingbirds of northern populations); otherwise, birds without retained feathers, without white in outer rectrices, and with complete gorgets may be of either age group and should be aged U/AHY (*Calypte*)

FIG 4. Incomplete gorgets in male hummingbirds; reference specimens are A (BCHU CAS65332), B (BCHU CAS65333), C (COHU CAS19324), D (COHU CAS19327). Birds can be aged as follows: A, SY/TY (HY/SY in *Calypte*); B, AHY/ASY (U/AHY in *Calypte*); C, HY/SY (*Calypte*); and D, possibly ASY/ATY (*Calypte*) but more study is needed.

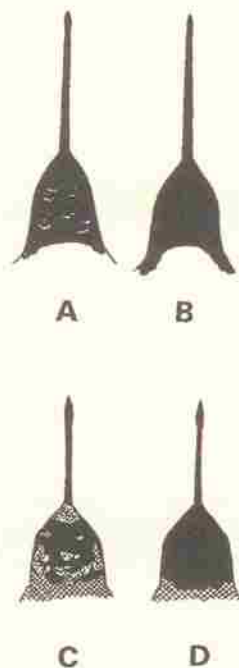
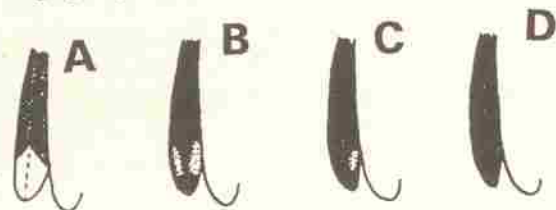


FIG 3. Variation of white in the outer rectrix (r5) of Broad-tailed Hummingbird. Some white may also appear in adjacent (r3-r4) rectrices as well. We suspect that birds with pattern B might be reliably aged SY/TY and birds with pattern D might be aged ASY/ATY, at least in northern populations, but more study is needed. White in the rectrices of SY/TYs of the other hummingbird species generally resemble that of pattern C.

or AHY/ASY. Ageing of 1st-basic females is more problematic, since retained rectrices and/or secondaries do not show marked age-specific differences when worn. We strongly suspect, however, that all birds with retained flight feathers can be reliably aged HY/SY (*Calypte*) or SY/TY, and hope that this can be confirmed by the study of known-aged birds in the field.

ACKNOWLEDGMENTS

We would like to especially acknowledge the efforts of numerous prior collectors for accumulating and preparing the specimens now at our disposal. The information that can still be gleaned from this incredible resource is vastly under-appreciated by most of today's ornithologists. We thank the following for access and assistance to specimen collections: Karen Cebra and Luis Baptista (CAS), Kimball Garrett (LACM), John Hafna and James Northern (MLZ), Ned Johnson and Carla Cicero (MVZ), Philip Unitt (SDNHM), and Walter Wehtje and Jon Fisher (WFVZ). William A. Calder and Stephen M. Russell provided unpublished data and feedback on a previous version of the manuscript. This is contribution # 678 of PRBO.

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