

INTRASPECIFIC AND INTERSPECIFIC VARIATION IN MOLT PATTERNS OF SOME TROPICAL HUMMINGBIRDS

F. GARY STILES

*Instituto de Ciencias Naturales, Museo de Historia Natural, Universidad Nacional de Colombia,
Apartado 7495, Bogotá D.C. Colombia*

ABSTRACT.—Sequences of flight-feather replacement were determined for 13 species of Costa Rican hummingbirds based upon capture-recapture data for 5 to 60 individually marked, adult individuals per species. A single sequence of primary molt occurred in 99% of all individuals, proceeding from innermost to outermost, except that the three outermost primaries molted in the sequence 8-10-9. For secondaries and rectrices, molt typically commenced with the innermost and/or outermost feathers and proceeded centripetally, but with much individual variation. Between 2 and 18 different sequences were observed in these tracts for the different species, the number of sequences per species being closely correlated with the number of molt records. Each species showed two or three common sequences and various rare ones; within at least one species, some individuals showed different sequences in successive annual molts. It is incorrect to postulate genetically fixed, rigid sequences of at least secondary and rectrix molt for these species, or even for individuals within a species. Bilateral asymmetry of feather replacement was very rare for primaries, but more frequent for secondaries and rectrices. For five species in which at least 30 records were available, the progress of molt over the entire plumage was examined, using primary molt as a standard. Molt in secondaries and rectrices commenced when four to six primaries had been replaced, and finished at about the same time as did primary molt. Wing and tail coverts commenced molt after, and finished before, the primaries. In all species, body molt proceeded continuously throughout the period of primary molt, with minor differences in timing in different tracts being far exceeded by individual variation. The major difference between species occurred in the timing of the molt of the throat and crown-forehead. The more specialized and differentiated were these areas into glittering crowns, frontlets and/or gorgets, the later they molted. Females of sexually dichromatic species, although lacking the glittering plumage of their males in these areas, nevertheless showed delays in head molt nearly or quite as great as those shown by males. *Received 13 April 1993, accepted 2 July 1993.*

HUMMINGBIRDS HAVE BEEN intensively studied over the last 15 to 20 years, but most work has focused on studies of foraging, behavior, and community structure. The molt of hummingbirds has received little attention, beyond specifying the place of molt in the annual cycles of various species (Stiles 1980, 1985) and a detailed study of molt timing in one species (Stiles and Wolf 1974). However, a number of interesting questions merit further study. How much variation in rates and sequences of molt exists within and among species? How does this variation relate to a species' foraging strategy, energy regimes, plumage patterns, or displays?

The few previous studies of molt in hummingbirds are mostly qualitative or anecdotal in nature. The only comparative studies are those of Ruschi (1962) on Brazilian species, and Wagner (1955) on several Mexican species. However, Ruschi's qualitative conclusions evidently

are based upon very cursory observations (see below), and the unusual molt sequences he described require confirmation. Wagner specified sequences of flight-feather replacement based on freshly collected specimens of several species. His conclusions regarding interspecific variation were based on unspecified (but evidently small) sample sizes, and he did not consider intraspecific variation in detail.

The most careful and thorough study on molt in hummingbirds was that of Williamson (1956) on the Anna Hummingbird (*Calypte anna*) in California. This is the only work to treat molt of both body and flight feathers of a large sample of specimens in sufficient detail for comparative purposes. A notable aspect of the molt of *C. anna* is the pronounced delay in the replacement of the brilliantly colored crown and gorget of the male, relative to the rest of the plumage. The extent to which this pattern is

peculiar to *C. anna* (in which these areas are very important in aerial and static displays; cf. Stiles 1982) needs to be evaluated through comparison of the molt sequence of a variety of species that differ in the degree to which these areas are specialized.

Here I evaluate the extent of inter- and intraspecific variation in molt sequences of several species of Costa Rican hummingbirds, with data from large samples of mist-netted birds. I present data on flight-feather molt for 13 species to quantify the variation in the molt sequences of the individual feathers. For five of these species that differ in the extent of glittering, specialized plumage, I present data on body molt to compare the relative timing of the replacement of different areas of the plumage between species. Only adult hummingbirds are considered here; I do not treat postjuvenile molt, which is highly variable among species in extent and timing (see Stiles 1980, Stiles and Wolf 1974).

METHODS AND MATERIALS

I determined sequences of flight-feather molt in wild hummingbirds, individually marked with aluminum bands or acetate leg tags, that were recaptured at least twice during the molt at intervals of two to six weeks. This method has the advantage that blood quills, so often lost or shriveled in prepared specimens, can be seen clearly (cf. Wagner 1955). Also, the accumulation of large samples is possible, avoiding the danger of biased conclusions due to accidental molt. Two or more recaptures, spaced through the molt, permit the entire sequence to be specified much more precisely than can be done with a single capture or a prepared specimen. Because most feathers in a tract are either old or fully grown at any given moment, their exact sequence of replacement can only be conjectured from a single observation.

Flight feathers were numbered as follows: primaries from 1 to 10 from innermost to outermost; secondaries from 1 to 6 from outermost to innermost; and rectrices from 1 to 5 from the central pair outwards. The stage of molt of each tract of flight feathers (primaries, secondaries, rectrices) was quantified by the method of Stiles and Wolf (1974), which in turn is a modification of the method of Pitelka (1958). An advantage of this approach is that each fully grown feather receives a score of 1 rather than some arbitrary number; thus, the total score for the tract equals the number of feathers (e.g. bird receives primary molt score of 10 upon completion of primary molt). This method treats each feather as a unit, ignoring differences in length or mass. Because there is little differ-

ence among hummingbird species in the relative sizes of the remiges (except for a few species with modified outer primaries, none of which are included in my study), interspecific comparisons are not affected. Species differ more in the relative lengths of the rectrices; such differences will not affect interpretation of molt sequences, but must be taken into account in quantifying molt rate, which will be treated elsewhere.

For molt of the head and body, I divided the plumage into 10 areas—5 dorsal (forehead, crown, nape, back, and rump) and 5 ventral (chin, throat, breast, belly, and sides-flanks)—plus wing and tail coverts. These areas were chosen to permit rapid examination and scoring (often a necessity during intensive netting operations) and correspond only approximately to the distribution of pterygiae. Molt was scored from 0 to 5 according to the number or proportion of feathers in the area that were obviously growing (partly or wholly enclosed in sheaths), as follows: (0) no growing feathers; (1) one or two growing feathers in entire area; (2) 2–10 growing feathers; (3) up to one-fourth of feathers in some stage of growth; (4) one-fourth to one-half of feathers growing; and (5) one-half or more of feathers growing.

Molt of the primaries was taken as the basis of comparison for molt in other areas since the sequence of molt in this tract is nearly invariable and easily quantified, and because molt in other areas rarely extends beyond the period of primary replacement (see below and Stiles and Wolf 1974). Thus, a primary molt score (the equivalent number of fully grown primaries) was computed, and scores for molt in other tracts were entered in the column corresponding to the primary stage (e.g. stage 6 includes all records of primary molt scores between 6.00 and 6.99). Cumulative mean molt scores of these areas were compared using Kolmogorov-Smirnov two-sample tests to evaluate relative differences in timing of different areas within species.

I obtained molt data from hummingbirds captured at the following Costa Rican localities: Finca La Selva, Provincia de Heredia (1968–1985, but mainly between 1971 and 1975); La Montura and Carrillo, Parque Nacional Braulio Carrillo, Provincia de San José (1980–1983, also 1989); Monteverde, Provincia de Puntarenas (1986–1989); Finca El Plástico, Provincia de Heredia (1987–1989); and the area of the Universidad de Costa Rica, Provincia de San José (1977–1989). Because I was mainly interested in primary molt during the La Selva study (see Stiles and Wolf 1974), my sample sizes for this tract are much larger than for any other. Although I obtained data on molt for 42 species in all, I present data here only on those species for which I determined the complete sequence of flight-feather replacement in at least 5 individuals (13 species), or for which I obtained data on molt in all body areas for at least 30 individuals, with records well distributed throughout the molt (5 species).

TABLE 1. Sequences of primary molt in 13 species of hummingbirds.

Sequence	Species ^a													Total
	P.s.	T.c.	C.u.	G.a.	H.j.	A.t.	L.c.	P.g.	P.l.	A.s.	E.n.	E.c.	L.h.	
12345678-10-9	273	145	48	34	24	23	22	15	12	12	11	8	8	635
12345678-9-10	1	1	—	—	1	—	—	—	—	—	—	—	—	3
1234567-10-8-9	1	—	—	—	1	—	—	—	—	—	—	—	—	2
1234567-10-9-8	1	—	—	—	—	—	—	—	—	—	—	—	—	1
12367458-10-9	—	—	—	1	—	—	—	—	—	—	—	—	—	1
Totals	276	146	48	35	26	23	22	15	12	12	11	8	8	642

^a Hummingbird species: P.s. = *Phaethornis superciliosus* (Long-tailed Hermit); T.c. = *Thalurania colombica* (Crowned Woodnymph); C.u. = *Chalybura urochrysis* (Red-footed Plumleteer); G. a. = *Glaucis aenea* (Bronzy Hermit); H.j. = *Heliodoxa jacula* (Green-fronted Brilliant); A.t. = *Amazilia tzacatl* (Rufous-tailed Hummingbird); L.c. = *Lampornis calolaema* (Purple-throated Mountain-gem); P.g. = *Phaethornis guy* (Green Hermit); P.l. = *Phaethornis longuemareus* (Little Hermit); A.s. = *Amazilia saucerottii* (Steely-vented Hummingbird); E.n. = *Eupherusa nigriventris* (Black-bellied Hummingbird); E.c. = *Eltoira cupreiceps* (Coppery-headed Emerald); L.h. = *Lampornis hemileucus* (White-bellied Mountain-gem).

RESULTS

Sequences of replacement of flight feathers.—The nearly invariable sequence of primary molt (99% of 642 records for 13 species; Table 1) is ascending, from the innermost (primary 1) to the third-from-last (primary 8), with the outermost preceding the next-to-outermost (i.e. 10 precedes 9). The very few deviant patterns involved rearrangements among the outermost two or three primaries, except for one *Glaucis aenea* in which molt of primaries 4 and 5 was unaccountably delayed in both wings (perhaps reflecting previous arrested or accidental molt).

For secondaries and rectrices, the situation is more complicated, at least at first sight. Seventeen different sequences of secondary re-

placement (Table 2) and 22 sequences of rectrix replacement (Table 3) were recorded; all species showed at least two sequences in each tract. In both tracts, the number of sequences observed correlated closely with the number of molt records for a given species (Spearman $r = 0.977$ and 0.817 for secondaries and rectrices, respectively; $P < 0.01$ for both). Taking all species together, three sequences of secondary molt, and three of rectrix molt, are much more common than all the rest, accounting for 70 and 73% of the molt records in the respective tracts. Within any given species, all three of these sequences typically are present (unless sample size is very small), but one or two of them usually account for one-half or more of all molt records. The species differ mainly in the relative fre-

TABLE 2. Sequences of secondary molt in 13 species of hummingbirds. Abbreviations for species as in Table 1.

Sequence	Species													Total
	P.s.	T.c.	C.u.	G.a.	A.t.	H.j.	L.c.	E.n.	P.g.	E.c.	P.l.	A.s.	L.h.	
615234	15	17	6	4	5	8	5	4	4	2	2	1	2	77
162534	8	6	5	7	6	4	1	2	2	1	1	3	—	47
612534	6	7	3	3	3	3	8	3	1	3	3	2	3	45
126354	2	4	3	5	2	—	2	—	—	—	—	—	—	18
162354	4	2	1	1	1	—	—	1	1	—	—	—	—	11
165234	2	4	1	1	—	—	—	—	—	—	—	—	—	8
651234	5	—	1	—	—	1	—	—	—	—	—	—	—	7
126534	—	1	1	2	—	1	—	—	—	—	1	—	—	6
651243	3	2	1	—	—	—	—	—	—	—	—	—	—	6
612354	3	1	—	—	—	—	—	—	—	1	—	—	—	5
162345	2	—	1	—	—	—	—	—	—	—	—	—	—	3
126345	2	—	—	—	—	—	—	—	—	—	—	—	—	2
162453	1	1	—	—	—	—	—	—	—	—	—	—	—	2
165243	2	—	—	—	—	—	—	—	—	—	—	—	—	2
123465	—	1	—	—	—	—	—	—	—	—	—	—	—	1
123654	—	—	—	—	1	—	—	—	—	—	—	—	—	1
162543	—	1	—	—	—	—	—	—	—	—	—	—	—	1
No. records	55	47	23	23	18	17	16	10	8	7	7	6	5	242
No. sequences	13	12	10	7	6	5	4	4	4	4	3	3	2	17

TABLE 3. Sequences of rectrix molt in 13 species of hummingbirds. Abbreviations for species as in Table 1.

Sequence	Species													Total
	P.s.	T.c.	C.u.	G.a.	H.j.	L.c.	A.t.	A.s.	E.n.	E.c.	P.g.	P.l.	L.h.	
12534	4	16	9	7	8	10	6	3	3	3	1	1	3	74
12354	2	15	6	3	9	5	4	4	2	3	—	—	1	54
15234	19	10	4	5	2	1	3	—	1	—	3	2	—	50
15243	5	1	—	1	—	—	1	—	—	—	1	—	—	9
51423	7	—	—	—	—	—	—	—	—	—	—	1	—	8
51234	1	—	1	—	—	—	1	—	1	—	1	2	—	7
12543	—	2	—	1	1	—	1	1	—	—	—	—	—	6
52134	2	—	1	1	—	—	—	—	—	1	—	—	—	5
51243	3	1	—	—	—	—	—	—	—	—	—	—	—	4
51342	3	—	—	1	—	—	—	—	—	—	—	—	—	4
15324	2	1	—	—	—	—	—	—	—	—	—	—	—	3
15423	3	—	—	—	—	—	—	—	—	—	—	—	—	3
54123	3	—	—	—	—	—	—	—	—	—	—	—	—	3
21534	—	1	1	—	—	—	—	—	—	—	—	—	—	2
12345	—	—	—	—	1	—	—	—	—	—	—	—	—	1
13245	1	—	—	—	—	—	—	—	—	—	—	—	—	1
13524	1	—	—	—	—	—	—	—	—	—	—	—	—	1
15342	—	—	—	1	—	—	—	—	—	—	—	—	—	1
21354	—	1	—	—	—	—	—	—	—	—	—	—	—	1
21534	—	1	—	—	—	—	—	—	—	—	—	—	—	1
23514	1	—	—	—	—	—	—	—	—	—	—	—	—	1
53124	1	—	—	—	—	—	—	—	—	—	—	—	—	1
53142	—	—	—	1	—	—	—	—	—	—	—	—	—	1
53421	1	—	—	—	—	—	—	—	—	—	—	—	—	1
54132	1	—	—	—	—	—	—	—	—	—	—	—	—	1
No. records	60	48	22	21	21	16	16	8	7	7	6	6	4	242
No. sequences	18	9	6	9	5	3	6	3	4	3	4	4	2	25

quency of these three "modal patterns" for both secondary and rectrix molt. The total number of sequences increases with sample size because of the progressive addition of rare sequences (Tables 2 and 3).

Despite the many sequences observed, there is an orderly pattern. In the secondaries (Table 2), molt always commenced at the extremes of the tract and progressed towards the center. Most of the variability in sequences reflected the relative timing of initiation of molt at either extreme: whether secondary 1 or 6 was the first to molt, and whether 2 or 5 then followed. In most species, secondary 6 was usually the first to be replaced, but in a few (*Glaucis aenea* and perhaps *Amazilia saucerrottei*) secondary 1 was first; in *A. tzacatl*, the two patterns were about equally frequent. In nearly all cases, secondary 4 was the last to molt, although rarely 3 or 5 was last, usually preceded by number 4 (Table 2).

In the rectrices, the central pair (number 1) usually is the first to be replaced, with the second-from-outermost pair (number 4) typically last. The outermost pair (5) usually is molted

early in the sequence, but is next-to-last in a considerable proportion of cases, and rarely is last. The species differ mainly in which of the three modal sequences is most common. In the genus *Phaethornis*, 15234 is the commonest pattern, and rectrix 5 usually molts early in the sequence. In all other species the commonest patterns are 12354 and 12534. It also appears that rectrix molt is more variable (i.e. for a given sample size, more patterns occur) in hermits than in nonhermits (Table 3).

Molt of the flight feathers usually was bilaterally symmetrical, but the frequency of asymmetry varied both between tracts and among species (Tables 4 and 5). In *P. superciliosus*, asymmetry was slight and infrequent in the primaries, but progressively more common and pronounced in secondaries and rectrices, respectively (Table 4). The same trends were shown in three other species for which less extensive data exist, including one other hermit (*G. aenea*) and two nonhermits (*Chalybura urochrysis* and *Thalurania colombica*). In general, bilateral asymmetry in flight feather replacement seemed about twice as frequent in hermits as in non-

TABLE 4. Bilateral asymmetry in molt of flight feathers in *Phaethornis superciliosus*.^a

Difference in molt score between right and left sides	Numbers of cases observed		
	Primaries	Secondaries	Rectrices
0.1	187	163	90
>0.1 to 0.5	15	23	72
>0.5 to 1.0	1	11	27
>1.0 to <2.0	0	5	10
2.0	0	0	4

^a Differences between tracts in degree of asymmetry tested by Kolmogorov-Smirnov two-sample tests: primaries and secondaries, $D_{\max} = 0.118$, ns; secondaries and rectrices, $D_{\max} = 0.360$, $P < 0.01$; primaries and rectrices, $D_{\max} = 0.478$, $P < 0.01$.

hermits, although due to small sample sizes the differences were not statistically significant (chi-square tests).

In *P. superciliosus*, I determined the sequence of flight feather replacement for a number of marked individuals over two or three successive annual molts. Often the same individual showed different sequences in successive years. For example, YRP showed secondary sequences of 615234 and 612534 in succeeding molts; OY showed 126534 and 612534; WGP showed 162534 and 162354; the most difference was shown by YB with sequences of 126345 and 615234. By contrast, WW showed the same sequence (651234) in three successive years; five birds showed 615234 in successive years, two showed 162534 and one, 651243. For rectrix molt, I have two cases of three consecutive years of data for a given individual: WW showed successive sequences of 51423, 15234, and 51423; and OY showed 54123, 51243, and 51234. In birds with two years of data, four showed 15234 in both years, five repeated three other sequences, and five changed sequences between years. Cases of an individual changing sequences of secondary or rectrix molt between years clearly are not rare: particular sequences often do not characterize individuals, much less species.

Timing of secondary, rectrix, and body molt relative to primary molt.—The five species considered here include one sexually monochromatic hermit (*P. superciliosus*) and four dichromatic nonhermits, males of which differ in the amount of specialized, glittering plumage. In *C. urochrysis*, males are dark iridescent green below, but lack glittering crowns or gorgets; males of *T. colombica* and *Heliodoxa jacula* have brilliant foreheads (frontlets), throats, and chests; and male *Lampornis calolaema* have highly differen-

TABLE 5. Bilateral asymmetry in molt of the flight feathers in four species of Costa Rican hummingbirds.

Feather tract	Molt ^a	
	Symmetrical	Asymmetrical
<i>Phaethornis superciliosus</i>		
Primaries	202	1
Secondaries	186	16
Rectrices	162	41
<i>Glaucis aenea</i>		
Primaries	24	1
Secondaries	21	2
Rectrices	17	5
<i>Chalybura urochrysis</i>		
Primaries	28	0
Secondaries	22	1
Rectrices	19	3
<i>Thalurania colombica</i>		
Primaries	48	0
Secondaries	44	1
Rectrices	45	6

^a Molt considered asymmetrical if molt scores of right and left sides differ by 0.5 or more. Asymmetry more frequent in hermits than in nonhermits in rectrices ($\bar{x} = 5.53$, 1 df, $P < 0.05$, Yates correction) but not in secondaries ($\bar{x} = 1.06$, ns).

tiated, glittering crowns and gorgets. For *T. colombica* and *H. jacula*, data also are available for females, which in the former lack glittering plumage, and in the latter are spangled with bright green below.

All five species commenced secondary molt when the equivalent of three to five primaries had been replaced, and all completed it at about the same time as they finished primary molt. There was little variation in mean values of secondary molt between species, but in each species there was considerable individual variation in the stage of secondary molt attained at a given primary molt stage (Fig. 1).

Rather more variation, both within and among species, existed in the timing of rectrix molt relative to primary molt (Fig. 2). In all species, this variability was greatest in the inception of rectrix molt; some individuals commenced it as early as primary stage 4, others not until stage 6 or even 7. The slow increase in mean rectrix molt score between primary stages 4 and 6 reflected mainly a variable proportion of birds that had not yet commenced rectrix molt (stage 0). Rectrix molt score increased rapidly from primary stage 7 onwards, and all nonhermits had essentially completed it by the time primary molt was finished. In *P. superciliosus*, rec-

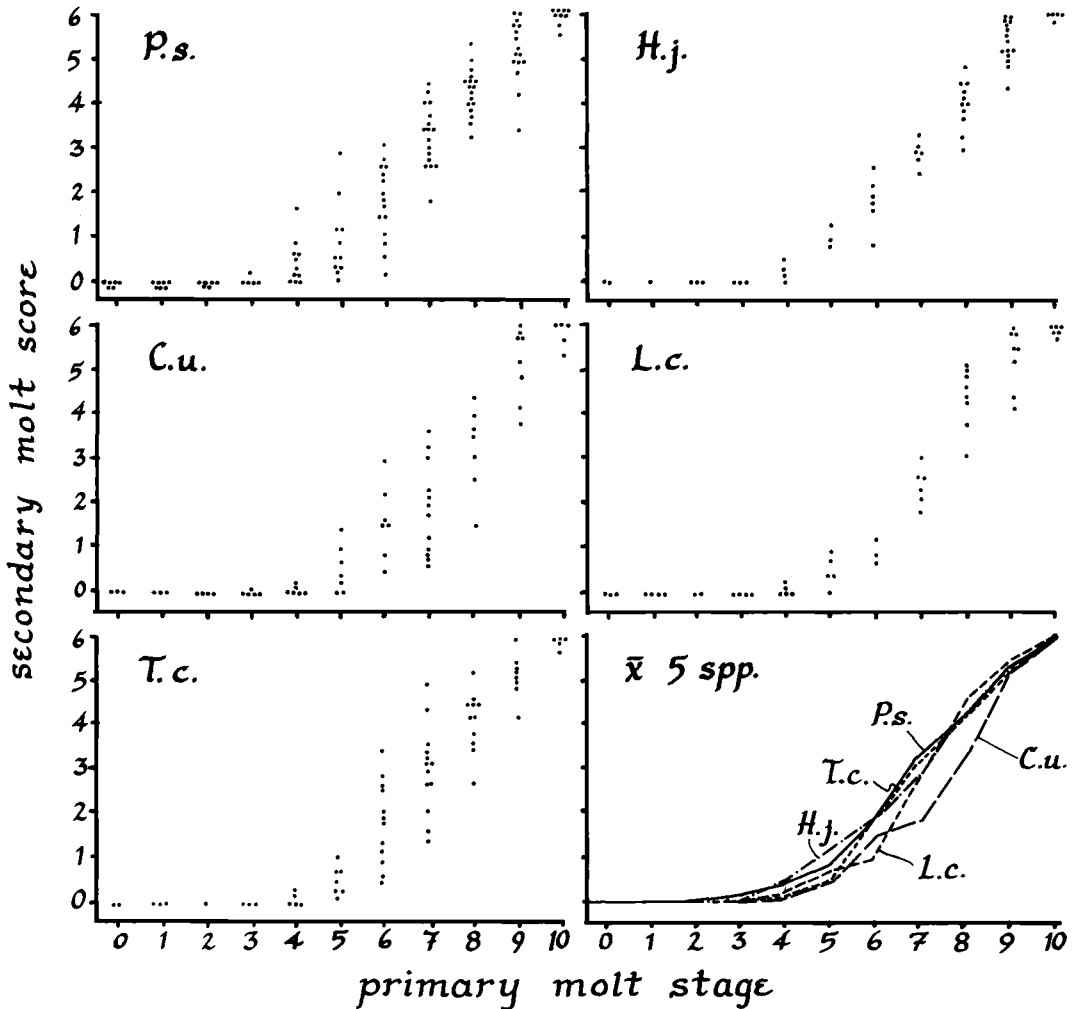


Fig. 1. Variation within and among five hummingbird species in secondary molt score in relation to primary molt stage. Each dot represents one molt record. Abbreviations for species as in Table 1. Lower right graph compares mean secondary molt scores for each primary molt stage.

trix molt often was not completed until after all primaries had been replaced (Fig. 2), usually because the greatly elongated central rectrices, in spite of being among the first to commence molt, were often late in finishing.

The wing coverts begin to molt by primary molt stage 2 or 3 (*C. urochrysis*, *H. jacula*) or 4 (other species). I do not consider this difference to be significant, as I did not distinguish primary from secondary coverts while taking the data, thus ignoring possible differences between tracts. However, in all species, molt of the wing coverts is completed by primary stage 8 in most individuals, thus somewhat earlier than the remiges themselves. Similarly, molt of

the tail coverts both starts (usually primary stage 3 or 4) and finishes (stage 7 or 8) earlier than does molt of the rectrices (Fig. 3, Table 6).

In all species, body molt commenced at about the same time as did primary molt; by the time primary stage 1 was attained, some species had replaced an appreciable proportion of the feathers (up to ca. 10%) in some body areas. Although my data on this point are limited, apparently in no species did the inception of body molt precede the dropping of the first primary by more than a week or so: I never encountered an adult bird with body molt in stage 2 or greater in any tract, and a primary score of 0. The sides, flanks, and usually the back were the first

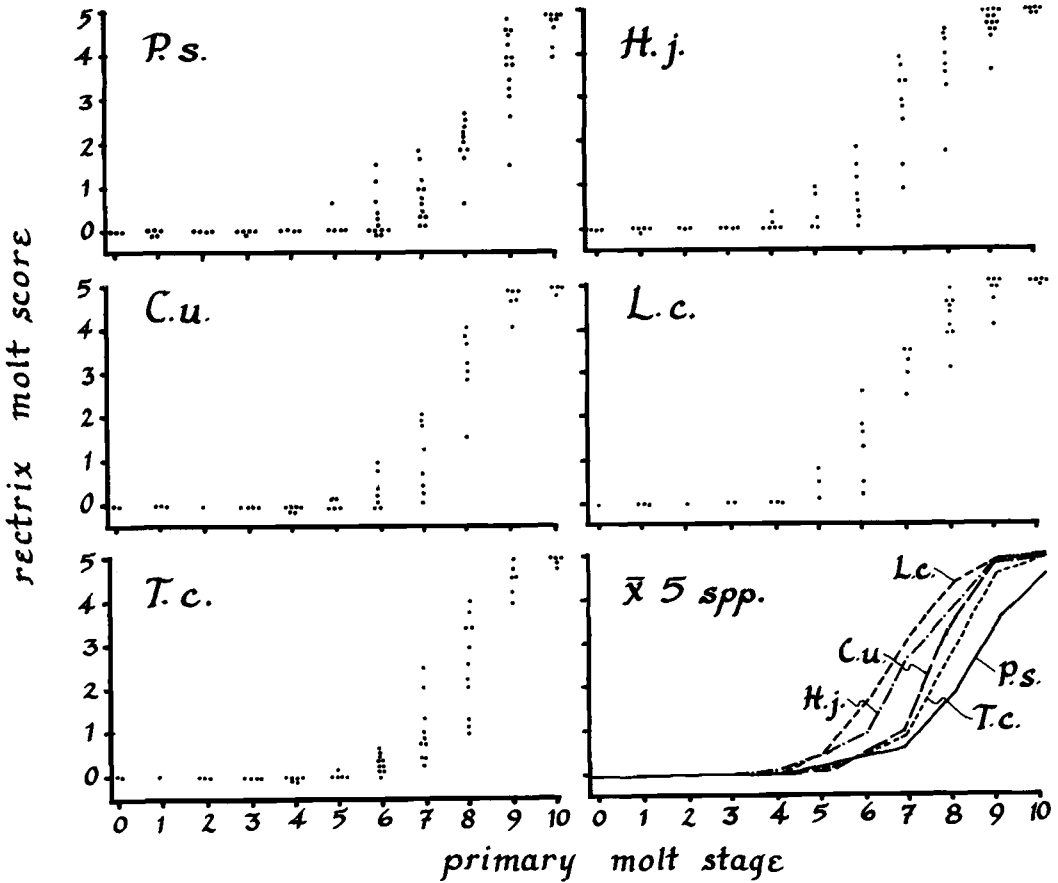


Fig. 2. Variation within and among five hummingbird species in rectrix molt score in relation to primary molt stage. Abbreviations for species as in Table 1; lower right graph compares mean rectrix scores.

body areas to commence feather replacement, with one-half or more of all individuals molting in these areas by primary stage 1, and most by 2 or 3 (Fig. 3).

Other body areas (breast, belly, rump, nape), although occasionally molting as early as primary stage 1, usually commenced at primary stage 2 or 3, occasionally 4. Once begun, body molt usually proceeded throughout the period

of primary molt, and at a fairly constant rate with respect to the latter. The peak of molt in all areas (the period with the highest proportion of feathers at some stage of growth) usually occurred between primary stages 5 and 7 or 8 in most individuals of all species. The mean differences in timing of molt of the different body areas within a species were usually minor, statistically insignificant, and far exceeded by

Fig. 3. Progress in molt of wing coverts, tail coverts, and various areas of body plumage (mean cumulative molt scores; see text) in relation to primary molt stage in five species of hummingbirds. Abbreviations for species as in Table 1. Other abbreviations: (d) dorsal areas, wing coverts; (v) ventral areas, tail coverts. Conventions for areas (dorsal/ventral): (dotted line) forehead/chin; (solid line) crown/throat; (short dashes) nape/breast; (dot-dash) back/belly; (long dashes) rump/flanks and sides; (medium dashes) wing/tail coverts. Note progressively later molt of head feathers as these show greater specialization for brilliant iridescence (from top to bottom in figure), and late start but early finishing of wing and tail coverts, with little variation among other body areas.

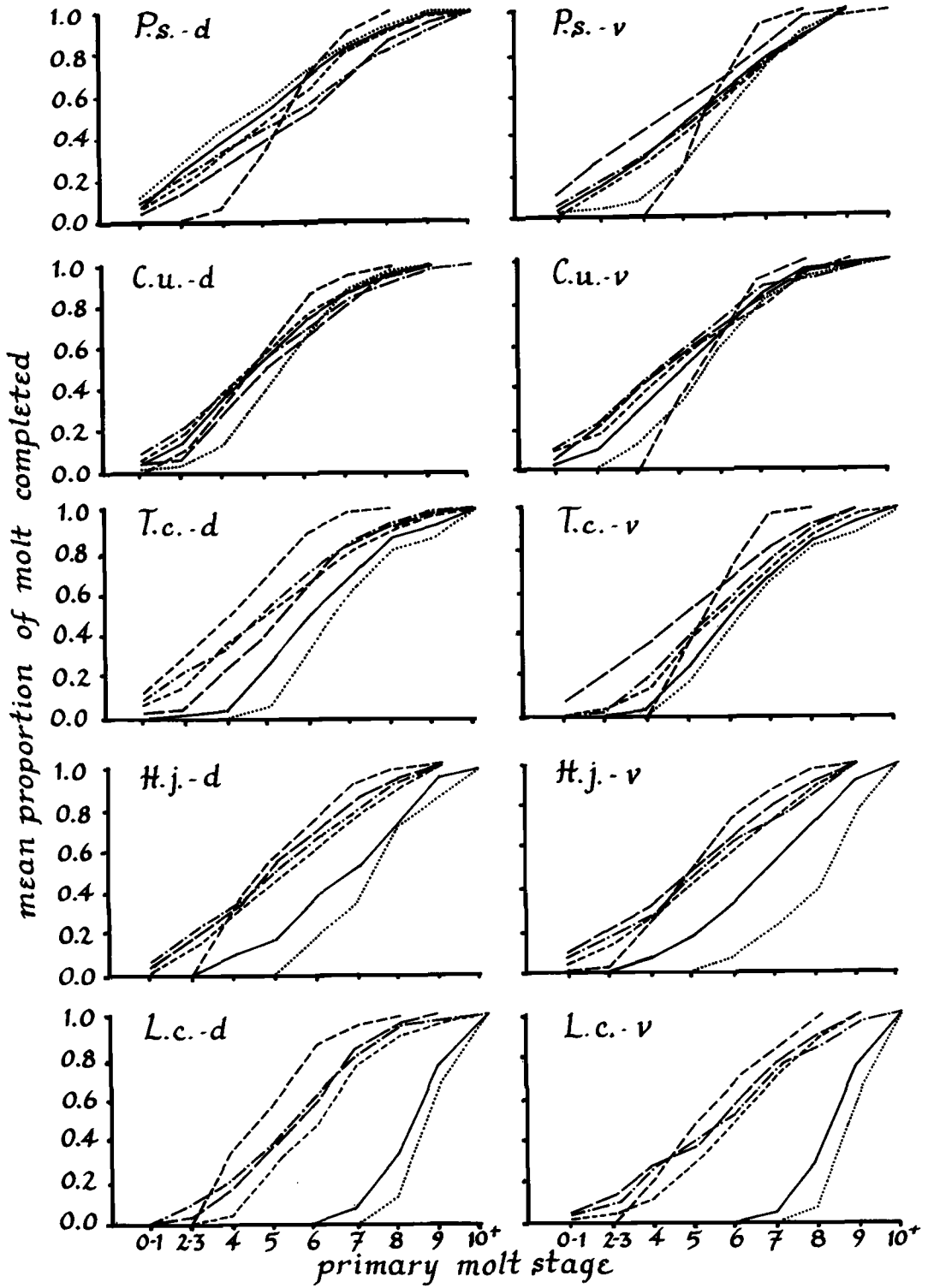


TABLE 6. Primary stages at which molt is initiated, at its peak, or completed in different body areas in five species of Costa Rica hummingbirds.

Body area	<i>Phaethornis superciliosus</i>			<i>Chalybura urochrysis</i>			<i>Thalurania colombica</i>			<i>Heliodoxa jacula</i>			<i>Lampornis calolaema</i>		
	Start	Peak	Finish	Start	Peak	Finish	Start	Peak	Finish	Start	Peak	Finish	Start	Peak	Finish
Wing coverts	ca. 5	5-6 or 7	ca. 8	3-4	4-6	A few 7, Some 8 most 2-3	A few 7, Some 8, ca. 5 most 2-3	3-6 or 7	8-9	2-4	6-7	8-9	3-4	4-6	8-9
Tail coverts	ca. 5	ca. 6	ca. 8	ca. 5	5-6	A few 8, ca. 5 most 9	A few 8, ca. 5 most 9	6-7	8-9	2-4	6-7	ca. 9	ca. 4	5-7	Most 8
Forehead	Half by 1, all by 5	4-6	9-10	A few 1, most 4-5	5-7	ca. 9	A few 1, most 5-6	6-8	ca. 10	6-7	8-9	>10	8-9	ca. 9	>10
Crown	Half by 1, all by 3	4-6 or 7	9-10	Half by 1, all by 3	4-7	ca. 9	A few 1, most 3-4	6-7	ca. 10	4-5	6 or 7-9	>10	6-8	8->9	>10
Hindneck	Most ca. 3	5-7	9-10	Half by 1, all by 3	4-6	9-10	Most 2-3	5-7	9-10	A few 1, most 2-3	5-7 or 8	9-10	3-5	6-7	ca. 10
Back	Most 0-1, all by 3	5-7	ca. 10	Most 0-1, all by 3	4-6 or 7	ca. 10	1-2	5-7	9-10	Most 0-1, all by 2	5-7	ca. 10	Most 0-1, all by 3	5-7	9-10
Rump	1-3	5 or 6-8	ca. 10	Some 0-1, all by 3	4-7	ca. 10	Rarely 1, most 4-5	5-7	9-10	0-1 or 2	5-7	ca. 10	Most 2-3	5-7	9-10
Chin	A few 1, most 4-5	6-7	ca. 10	Most 4	6-7 or 8	>10	6-7 or 8	ca. 9	ca. 10	ca. 8	>9	>10	ca. 8	>9	>10
Throat	Some 0-1, most 2-3	4 or 5-7	ca. 10	Some by 1, all by 4	5-7 or 8	9-10	4-5	5-8	ca. 10	4-5	6-9	>10	ca. 8	8-10	>10
Breast	Some 0-1, most 2-3	5-8	ca. 10	Most by 1, all by 3	4-7	ca. 10	2-4	5-7 or 8	ca. 10	Some 0-1, all by 3	6-8	ca. 10	Some 0-1, all by 3	5-8	ca. 10
Belly	Half 0-1, all by 3	5-8	ca. 10	Nearly all 0-1	4-6 or 7	ca. 10	2-3 or 4	Most 6-7	ca. 10	Some 0-1, all by 3	5-7	ca. 10	Some 0-1, all by 3	4-7	ca. 10
Flanks + sides	Most 0-1	5-8	ca. 10	Most 0-1, all by 2	4-7	ca. 10	Most 0-1, all by 2	5-7	ca. 9	Most 0-1, all by 2	5-7	ca. 10	Most 0-1, all by 2	5-7	ca. 10

the amount of individual variation. The mean timing of the replacement of wing and tail coverts did differ significantly from that of most body areas, typically starting later and finishing earlier (Figs. 3, 4; Table 6) with respect to the primaries.

I found much more variation between species in the timing of the molt of the forehead, crown, chin, and throat (Fig. 3). In general, the greater the degree to which these areas were differentiated into specialized glittering areas, the later they were molted relative to the primaries (and other body areas). The hermit *P. superciliosus* lacks glittering feathers in these areas but does show a contrasting buffy stripe on the throat. Male *C. urochrysis* have dull crowns, and their uniformly iridescent green underparts lack highly glittering areas. Molt of the crown and forehead, and of the chin and throat, did not differ significantly in timing from that of adjacent body areas in either species (Fig. 4, Table 6).

In *T. colombica* males, a brilliant purple frontlet is set off by a velvety black crown; the anterior underparts are brilliant green, the lower breast and belly violet. Molt of the forehead was significantly later than that of the back and nape, that of the crown only slightly so; the chin and throat molted only slightly later than did the breast and belly. Male *H. jacula* have very brilliant green frontlets and anterior underparts, with a brilliant purple spot on the lower throat. Delay in the molt of these areas was greater relative to the primaries than in *T. colombica*, but only the chin and forehead differed significantly from other body areas in timing (Figs. 3 and 4, Table 6).

The delay in head molt was greatest relative to the body in male *L. calolaema*, which have very strongly differentiated, glittering crowns and gorgets (Fig. 3). Replacement of these areas did not commence until primary stage 7 or 8, and was completed well after the end of primary molt, differing highly significantly from the timing of molt of the body (Fig. 4, Table 6). In four males I noted some molt of the forehead and chin at least one month after the completion of primary molt.

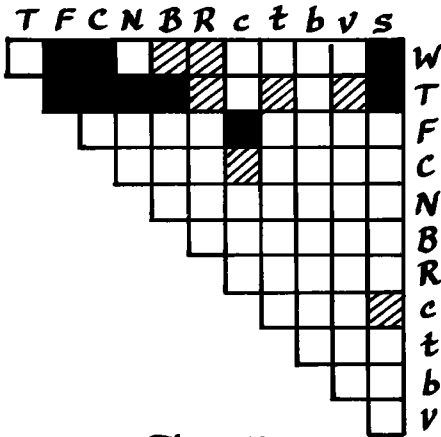
In the monochromatic *P. superciliosus*, there was no indication of any difference in the timing of head molt between the sexes. In *T. colombica* females, the crown is dull and the throat and chest are a contrasting, but not brilliant, pale gray. There was no detectable difference

in the timing of the chin, throat, or crown between the sexes; the forehead (frontlet) of males molted later than did that of females, but the difference falls just short of statistical significance ($0.10 > P > 0.05$), probably due to the small sample (17) of females. In *H. jacula*, head molt of males was at most slightly later than that of females and no differences approached statistical significance (Fig. 5). I have data for only two female *L. calolaema* in the final stages of primary molt: both were replacing many feathers on the chin, throat, forehead and crown at primary stages 6 to 8. In addition, I did not detect head molt in two females that had recently completed primary molt. There might be a greater sexual difference in molt of these areas in this species, but more data are needed to substantiate this.

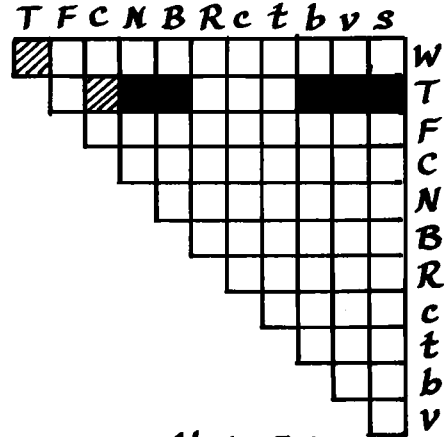
DISCUSSION

The sequences of flight-feather replacement in hummingbirds resemble those of most other birds, though with certain peculiarities that are explicable in terms of their highly specialized manner of flight. Molting the primaries in ascending order (i.e. innermost to outermost) is the most general avian pattern; only hummingbirds regularly invert the order of the outermost two primaries (Stresemann and Stresemann 1966, Payne 1972). This is apparently an adaptation to maintain the aerodynamic efficiency of the wingtip during feather replacement, this part of the wing being especially important in the hovering flight of hummingbirds (Greenewalt 1960, 1975). The centripetal sequence of secondary molt and the initiation of secondary replacement only after primary molt is well advanced are also widespread patterns, among flying birds, that serve to avoid creating large gaps in the flight surface (Stresemann and Stresemann 1966). The generally centrifugal (center outward) pattern of rectrix molt, seen in most birds, is varied in hummingbirds by having the outermost rectrix usually molting early in the sequence rather than last. In most hummingbirds these are the longest rectrices even if the tail is not obviously forked; perhaps they are especially important in providing lift or maneuverability. The virtually invariable sequence of primary replacement, and the progressively greater degree of variability and asymmetry in molt of the secondaries and rectrices, probably reflect the rel-

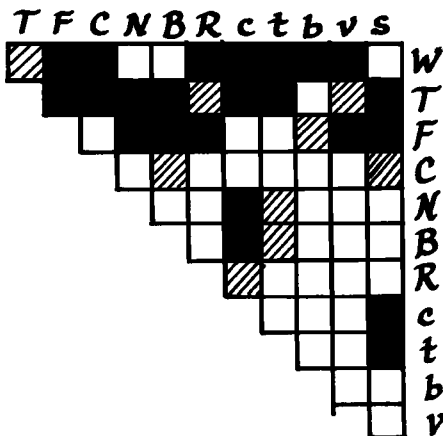
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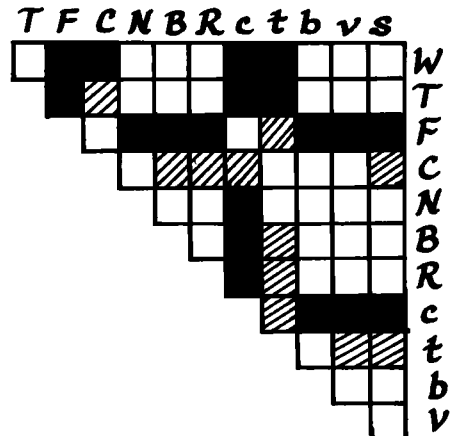
C.u. ♂♂



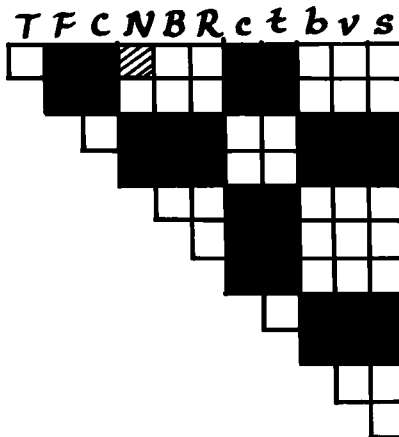
T.c. ♂♂



H.j. ♂♂



L.c. ♂♂



- W = wing coverts
- T = tail coverts
- F = forehead
- C = crown
- N = nape
- B = back
- R = rump
- c = chin
- t = throat
- b = breast
- v = belly
- s = sides-flanks

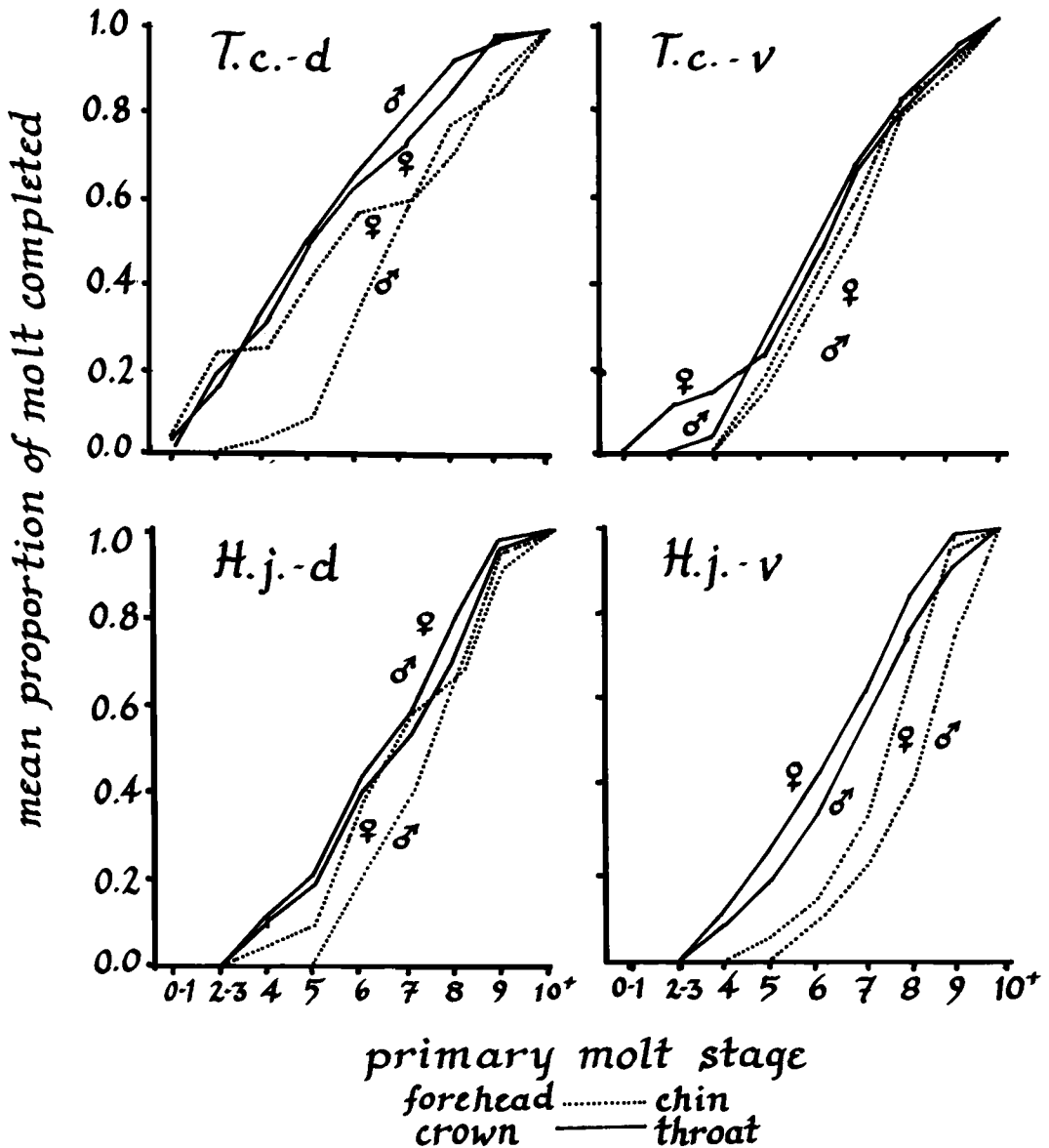


Fig. 5. Progress in molt of head areas (mean cumulative molt scores) for male and female *Thalurania colombica* and *Heliodoxa jacula*. Abbreviations for areas as in Figure 3. Although lacking the specialized iridescence of males, females delay molt of these areas nearly as much as do males (differences are not statistically significant).

ative importance of these feathers in flight. Along with swifts, hummingbirds have the smallest relative forearm length and secondary area of any flying birds. The great variation in

length and form of the rectrices in hummingbirds also suggests that their importance in flight per se might be less than in many other birds.

In the only other detailed comparative study

←

Fig. 4. Degrees of difference between cumulative molt scores of different plumage areas, as determined by Kolmogorov-Smirnov two-sample tests. Solid squares indicate $P < 0.01$; hatched squares indicate $P < 0.05$; open squares indicate $P > 0.05$ (no significant difference).

of molt sequences in hummingbirds, Wagner (1955) concluded that each species was characterized by a particular sequence of secondary and rectrix replacement. He cited four sequences of rectrix molt, three of which (each supposedly characterizing one or two species) are precisely the three most common sequences I found. The fourth, 12345, considered to characterize four species, was shown by only 1 of 242 individuals in my entire study! For the secondaries, Wagner mentioned three patterns, only one of which (with molt commencing more or less simultaneously in the innermost and outermost secondaries) is clearly compatible with my observations. I never encountered either of the other two sequences he reported (123456, and a centrifugal sequence with molt commencing in the central secondaries and progressing towards the extremes). In the same species reported as showing the latter sequence (*Calothorax lucifer*), Wagner also cited an unusual primary sequence, with primaries 3 and 4 being dropped before 1 and 2, which again I have never encountered. I have limited data on only one of the species studied by Wagner, but my results are decidedly at variance with his. In this species, *Eugenes fulgens*, he reported a secondary sequence of 123456 and a rectrix sequence of 12345. In three Costa Rican birds, I recorded sequences of secondary replacement of 126354 in two, and 162354 in the other; rectrix sequences were 12354 in two and 15234 in the third. The species for which Wagner reported molt sequences most different from those I found was *Calothorax lucifer*. While I have never studied this species, I have data for several species in the allied genera *Philodice* and *Selasphorus*, and Williamson (1956) gave detailed information on molt sequences in the probably more distantly related *Calypte anna*. In all of these species, molt sequences are entirely consistent with those I report here.

I believe that the discrepancies between Wagner's conclusions and mine are best explained by differences in our respective methods rather than in having examined different species. In particular, I am sure that Wagner's statement that a single sequence of secondary or rectrix molt characterizes a given species can only be due to very small sample sizes (and Wagner himself mentioned the occurrence of occasional "aberrant" sequences). Since Wagner based his conclusions on collected specimens, he might have been led into assuming greater uniformity

of sequences than was actually the case. Because only two or three feathers in any flight feather tract are actually growing at any one time, a single specimen cannot provide data on the full sequence in that tract. He very likely assumed that fully-grown feathers in one specimen had molted in the same order as the same feathers that, in another specimen, were in different stages of growth (or that feathers yet to molt in one specimen would follow the same order as in another in which they were actually molting). His report of sequences like 123456 (secondaries) or 12345 (rectrices) probably reflected insufficient data on molt at the extremes of these tracts. In particular, he might have assumed, on the basis of birds molting only the inner rectrices, that the outer ones would continue in a centrifugal sequence, since this is the most common pattern in birds in general. Also, since the innermost two secondaries have more iridescent color than the rest, he might have assumed that they were the freshest on a bird that had completed secondary molt. There are, therefore, enough pitfalls in Wagner's methods to account for the differences in our conclusions, but definitive proof of this will only be possible when the same species are restudied by repeatedly examining the same individual birds at different stages of their molts.

Little can be concluded regarding the details of molt sequences from the writings of Ruschi (1962), since his conclusions tend to be vague, qualitative, and evidently based on very cursory observations. For instance, he stated that the primaries were molted from innermost to outermost with the "first" (i.e. number 10) being the last to molt—evidently overlooking the inversion of the sequence of the two outermost primaries mentioned by all other observers of molt in hummingbirds.

The overall pattern of flight feather molt reported here, with the secondaries and rectrices commencing towards the middle of primary molt and finishing about the same time as the primaries, was also found by Williamson (1956) in *C. anna* and Wagner (1955) in *C. lucifer* (although Wagner stated that "shedding of rectrices generally follows when wing molt is nearly concluded," which is at odds with his fig. 1). Ruschi (1962) stated that primaries molt before secondaries in Brazilian species, but it is not clear whether he is referring to the entire molt or (as I suspect) to its initiation in these two tracts.

The overall pattern of body molt reported by Williamson (1956) in *C. anna* is virtually identical to that of the five species I studied (Fig. 3, Table 6), allowing for differences in our respective methods of quantifying molt. Wagner (1955) stated that "molt of the contour feathers begins toward the end of the molting of the remiges" in Mexican hummingbirds, a conclusion strongly questioned by Williamson (1956). I suspect that Wagner might have been misled by delayed molt of the brilliant crowns and/or gorgets of several species (e.g. *E. fulgens*, *C. lucifer*). Ruschi (1962) cited rapid molt, with most feathers shed nearly simultaneously, in the cephalic, humeral, crural, and caudal tracts of Brazilian hummingbirds—in my view an overstatement. He contrasts this with gradual, symmetrical molt in alar, ventral, and spinal tracts. In my experience, molt in the former two tracts is only approximately symmetrical, certainly much less so than in the remiges. Clearly, the molt patterns of Brazilian hummingbirds require further study.

In male *C. anna*, the crown and gorget are even more brilliant and differentiated than in male *L. calolaema*, and molt of these areas apparently is delayed to an even greater degree with respect to the rest of the plumage (Williamson 1956). There is also a much greater difference in timing of molt of these areas between male and female *C. anna* than I found in *T. colombica* and *H. jacula*, such that the annual molt in the former species might require up to two months more for males than for females.

The adaptive value of the delayed molt of brilliantly colored crown and/or gorget feathers is probably to assure that the bird enters the subsequent breeding season with this plumage at its most brilliant, unaffected by wear (Williamson 1956). In most hummingbirds molt follows closely after breeding, with little or no overlap between the two at the individual level (Stiles 1980, 1985, Williamson 1956; but see Stiles and Wolf 1974). The amount of delay in the molt of these plumage areas evidently is related to their degree of differentiation, but another factor to consider is the length of the interval between breeding seasons. For *C. anna* in California, this "quiescent period" is four to six months long (Williamson 1956, Stiles 1973), but for many tropical species it may be much shorter. In particular, Feinsinger (1977) stated that *L. calolaema* breeds year-round at Monteverde. Although this is probably an overstatement, it

is virtually certain that the quiescent period, and hence the time available for the delay of crown and gorget molt by males prior to the next breeding season, is much shorter in this species than in *C. anna*. In general, the delay in the molt of these glittering areas, which are important in displays (cf. Stiles 1982), would appear to be an adaptation analogous to the prealternate (prenuptial) molt in various other groups of birds (Palmer 1972).

No comparable data are available on intra- and interspecific variation in molt sequences for any other birds. A very detailed, comparative study of molt in British corvids was reported by Seel (1976), based upon large samples of freshly killed birds. These corvids also initiated primary molt before that of the secondaries and rectrices, and commenced body molt at about the same time as, or slightly later than, they began to molt the primaries. Wing molt was more rigidly structured than was molt in other areas, much as I found in hummingbirds. Seel also described inter- and intraspecific variations in the timing of molt in different tracts comparable to what I report here, although he did not attempt to specify exact sequences of flight-feather molt. More precise comparisons are difficult because of differences in the way molt was quantified; his emphasis was on the population, mine on the individual.

Willoughby (1991) recently documented a considerable degree of intra- and interspecific variation in the pattern and timing of head and body molt in six species of *Spizella* sparrows. Differences in molt between species during the breeding season were related to exposure to abrasive vegetation and, to a lesser extent, to aridity. Supplemental feather replacement occurred especially in those plumage areas carrying markings important in recognition and displays and, thus, represents another analogue to the delay in crown and gorget molt in some male hummingbirds. Intraspecific variation in patterns of head and body molt among these sparrows was in some cases at least comparable to what I found in hummingbirds, although our methods of quantifying molt differed. Working with large series of specimens, Willoughby treated body molt in greater detail but did not study sequences of flight feather replacement.

The degree of variability that I found in sequences of flight-feather replacement in hummingbirds has implications for possible mechanisms that control such sequences, a subject

still poorly understood (Payne 1972). One prevalent theory is that of Ashmole (1968), which postulates that the sequence of remex molt is controlled by fixed, presumably genetically determined rhythms in each feather follicle, the rhythms of different follicles being offset to a similarly predetermined degree. At least for the secondaries and rectrices of hummingbirds, the degree of individual variation—and especially the occurrence of different sequences in successive years in many individuals—clearly is incompatible with such a mechanism. My data accord better with the older hypothesis of genetically and/or physiologically determined “molt centers” or sites of molt initiation, combined with a somewhat flexible or temporally variable pattern of local retrocontrol effects, in the expression of sequential molt of the flight feathers (cf. Miller 1941, Ashmole 1968, Payne 1972).

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