MOLT AND AGE DETERMINATION IN WESTERN AND YELLOWISH FLYCATCHERS

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TEN years ago I presented a review of research on molts in tyrannid flycatchers of the genus *Empidonax*, in a paper that included original data for five species (Johnson 1963b). Since that time very little has been published on this aspect of the biology of these flycatchers, although Mumford (1964: 46) and Traylor (1968) have added new details to data available for the Acadian Flycatcher (*Empidonax virescens*).

In the present paper I describe molt patterns and criteria for determining age in two close relatives in the genus *Empidonax*, the Western Flycatcher (*E. difficilis*) and the Yellowish Flycatcher (*E. flavescens*). The molts of these species have not been studied previously in any detail. This work was undertaken to gather background information necessary for the proper interpretation of size variation in a systematic analysis of this difficult group (Johnson MS). Finally I consider patterns and progress of cranial development in these flycatchers and offer a new hypothesis to explain retarded pneumatization of the skull roof in birds.

MATERIALS AND METHODS

Approximately 2,100 specimens of both species, representing all seasons and areas of geographic occurrence, were examined carefully under a magnifying lamp for evidence of molt and to determine degrees of plumage wear. Study was facilitated by the concurrent use of a strong microscope lamp to illuminate feather bases while rows of feathers were parted with a dissecting needle. Molt stages used are the same as those defined for *Empidonax hammondii* (Johnson 1963a: 124–128).

For the Western Flycatcher, emphasis is on *E. d. difficilis*, the form for which sufficient samples are available. Most migrating and wintering examples of the nominate race may be separated by features of size and coloration from resident Mexican forms of the species (Johnson MS). Furthermore, geographic contact on the wintering grounds between *E. d. difficilis* and the interior complex of larger and/or darker forms (*E. d. hellmayri-E. d. occidentalis*) is minimal because *E. d. difficilis* winters in the main at low elevations along the western coast of Mexico, in essential allopatry with the other forms wintering in the uplands of interior Mexico.

Age categories are defined as follows: juvenile, any individual that has not completed the postjuvenal molt; immature, a bird between the end of the postjuvenal molt and the first prenuptial molt; first-year bird, an individual between the first prenuptial molt and the end of the first postnuptial molt; and adult, any bird that has completed the first postnuptial molt in the life cycle.

Sketches of crania showing areas with incomplete pneumatization were drawn in the field when study skins were prepared. Additional skulls were examined
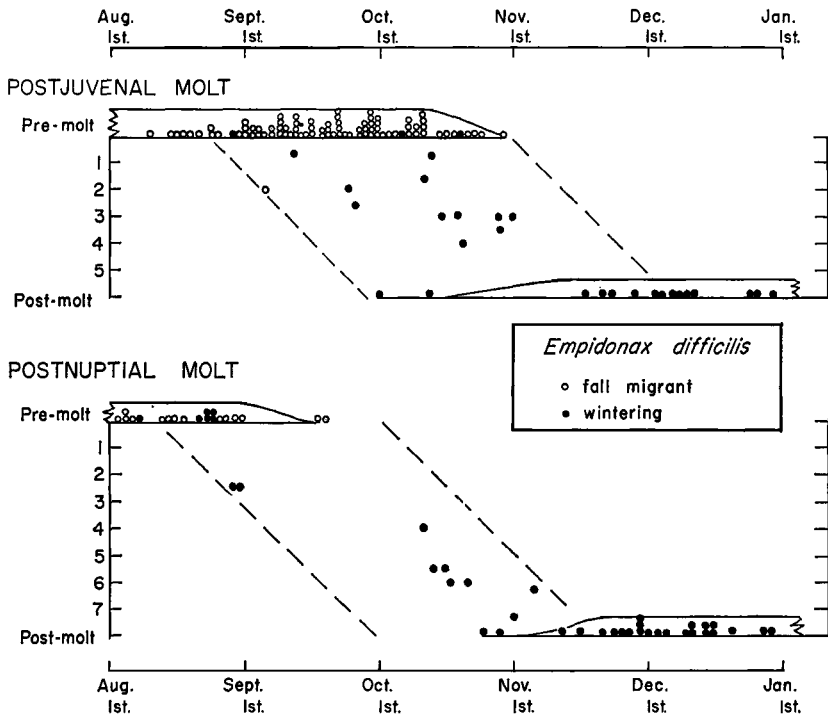
Aug.   Sept.   Oct.   Nov.   Dec.   Jan.
1st.   1st.   1st.   1st.   1st.   1st.

POSTJUVENAL MOLT

Pre-molt
1
2
3
4
5
Post-molt

POSTNUPTIAL MOLT

Empidonax difficilis

o fall migrant
• wintering

Pre-molt
1
2
3
4
5
6
7
Post-molt

Aug.   Sept.   Oct.   Nov.   Dec.   Jan.
1st.   1st.   1st.   1st.   1st.   1st.

Figure 1. Timing of postjuvenal and postnuptial molts in *Empidonax difficilis difficilis* in relation to the timing of the fall migration and appearance at localities of winter occurrence. Slanted dashed lines represent the estimated temporal limits of molt for all populations of the species. Numbered stages of molt follow Johnson (1963a: 124–128).

in the skeletal collection of the Museum of Vertebrate Zoology. Measurements of the outer seven primary feathers were taken from the bend of the wing to the tip of each feather, as described previously (Johnson 1963a: 90–91).

Nomenclature used here follows a systematic revision of this complex that is nearing completion (Johnson MS). In this revision biologic criteria are presented that support the specific separation of *E. difficilis* and *E. flavescens*.

MOLT CYCLES

WESTERN FLYCATCHER (*Empidonax difficilis difficilis*)

Apparently because there has been no previous concerted study of molt based upon large series of specimens of the Western Flycatcher, the limited information in the literature on cycles of feather replacement in this species is largely erroneous. Bent (1942: 250) stated that the "young birds molt the body plumage late in the fall and have a complete prenuptial molt in late winter or spring." Continuing, he re-

TABLE 1

Average Number of Feathers Replaced During the Postjuvenal Molt[1]

Form and sample size		Secondaries	Greater secondary coverts	Middle secondary coverts
Empidonax d. difficilis				
Northern pops.[2] (42)		1.38	1.62	0.71
Central pops.[3] (27)		1.26	1.19	0.74
Southern pops.[4] (35)		0.46	0.97	0.57
Empidonax d. hellmayri				
Northern pops.[5] (18)		5.06	5.89	5.44
Central pops.[6] (28)		4.93	6.07	5.14
Southern pops.[7] (41)		3.88	3.41	3.07
Empidonax f. salvini	(15)	2.80	1.60	3.87
Empidonax f. flavescens	(23)	1.22	1.04	2.61

[1] Based on first-year birds taken on their breeding grounds.
[2] Alaska and British Columbia.
[3] Washington and western Oregon.
[4] California.
[5] Alberta, Montana, Wyoming, and South Dakota.
[6] Nevada, Utah, and Colorado.
[7] Arizona, New Mexico, Texas, and Coahuila.

ported that the "adults seem to follow a similar sequence, with perhaps a renewal of the flight feathers during the winter." As described beyond, these statements are at complete variance with the facts. Others have described the postjuvenal molt as occurring before the fall migration (Miller and Stebbins 1964: 127; Ralph 1968). It is true that limited replacement of body plumage in some individuals may occur prior to fall migration, but typically the entire fall molt of all age groups takes place on the wintering grounds in Mexico. Finally, Phillips (1966) wrote that the Western Flycatcher has a single annual molt, when in fact both young and adults have two molts a year, one of which is the limited prenuptial molt in the spring.

Postjuvenal molt.—Occurs on the wintering grounds between early September and mid-November (Figure 1). This molt varies greatly in extent; some individuals replace only scattered body plumage, whereas others replace all body plumage and variable numbers of flight feathers and coverts (Table 1). Geographic variation in postjuvenal molt is discussed beyond.

Prenuptial molt.—This molt is usually very slight in the nominate race of the Western Flycatcher. Only the body plumage is involved; most individuals molt a few scattered feathers on the throat, breast, and dorsum. The prenuptial molt occurs from early March to early May on the wintering grounds. Both adults and birds hatched the previous summer undergo this molt. The adults molt somewhat ahead of the first-year birds, which is to be expected in view of the timing of their preceding fall molts.

Postnuptial molt.—The postnuptial molt of *E. d. difficilis* occurs from mid-August to mid-November on the wintering grounds (Figure 1) and is complete in all individuals.

Timing of molt and migration.—The nominate race of the Western Flycatcher resembles the Dusky Flycatcher (*E. oberholseri*) and the Gray Flycatcher (*E. wrightii*) in that both the postjuvenal and post-nuptial molts occur after migration, on the wintering grounds in Mexico (Johnson 1963a, 1963b). In contrast to those species, the Western Flycatcher molts more rapidly, over a period of approximately 3 months on a population basis, instead of extending the molt over roughly 4 months, and into the winter, as in *E. oberholseri* and *E. wrightii*. In Figure 1 the relation between timing of migration and timing of molt is shown for both juveniles and for birds that are at least 1 year old. Note that virtually all of the birds from the western United States taken past early September are juveniles of the year, some of which linger into late October. Worn juveniles arrive in Mexico as early as late August, whereas worn adults may arrive in early August. Juveniles of *E. d. difficilis* may be fully grown and independent of their parents by mid- to late June and seem to have more than sufficient time to complete the postjuvenal molt on the hatching grounds prior to migra-tion, even after consideration of the possibility in Western Flycatchers of a relatively extended maturation period as discussed by Morehouse and Brewer (1968) for kingbirds (*Tyrannus*). Yet for reasons that remain obscure the postjuvenal molt occurs on the wintering grounds in Mexico. Nonetheless, despite the present lack of a convincing explanation for the scheduling of molts in this fashion, it is assumed that the manner in which important events such as molts are programmed in the lives of the various species of *Empidonax* has definite adaptive value.

YELLOWISH FLYCATCHER (*Empidonax flavescens*)

The only published data on molt cycles of the Yellowish Flycatcher are the comments of Dickey and van Rossem (1938: 381) for *E. f. salvini* (discussed under *E. f. "dwighti"*) in El Salvador that, "As in most other species of *Empidonax* the juvenal remiges and rectrices are

TABLE 2

NUMBER OF RECTRICES REPLACED IN POSTJUVENAL MOLT[1]

	0	1	2	3	4	8	12
E. d. difficilis (N = 104)	97	2	2	1	1	—	1
E. d. hellmayri (N = 101)	89	3	5	—	—	—	4
E. f. salvini (N = 16)	6	—	1	—	—	1	8
E. f. flavescens (N = 28)	14	—	—	—	—	—	14

[1] Based on first-year birds taken on their breeding grounds.

retained through the first winter.... Material to outline the spring molt is lacking, but it is certainly not very extensive, for May examples from Volcan de Santa Ana are all in worn plumage." These findings are at variance with the results of my study. For one thing, at least half of all juveniles of both races of *E. flavescens* replace all their rectrices in the postjuvenal molt (Table 2).

Insofar as is known this species is sedentary and all molts occur on or near the breeding areas. Because comparatively few specimens of actively molting Yellowish Flycatchers have been preserved in museum collections, for certain aspects of the analysis I have had to combine data for *E. f. salvini* with those for *E. f. flavescens* in the following accounts. Thus, it is unfortunate that any subtle differences that may exist between the two forms in timing and/or extent of molts cannot always be demonstrated by the present analysis.

Postjuvenal molt.—This molt takes place between June and early October (Figure 2) and is therefore more protracted on a population basis than the comparable molt in *E. difficilis*. Whether an individual of *E. flavescens* has a more protracted postjuvenal molt than an individual of *E. difficilis* is uncertain. The latest date for the occurrence of postjuvenal molt is 10 October as represented by the type specimen of *E. f. salvini*. Only body plumage may be involved, but more often a variable number of rectrices, inner secondaries, and wing coverts also are replaced (Table 1). Many birds replace all of their rectrices in the postjuvenal molt (Table 2).

Prenuptial molt.—A prenuptial molt seems to be lacking in the Yellowish Flycatcher, an exceptional situation among the seven species of *Empidonax* for which relatively complete information on molt cycles is available.

Postnuptial molt.—This molt occurs between mid-June and early October (Figure 2) and is complete in all individuals. On a population basis the molt occupies approximately 3½ months and thus may take an estimated 3 weeks longer than the postnuptial molt of *E. difficilis*.

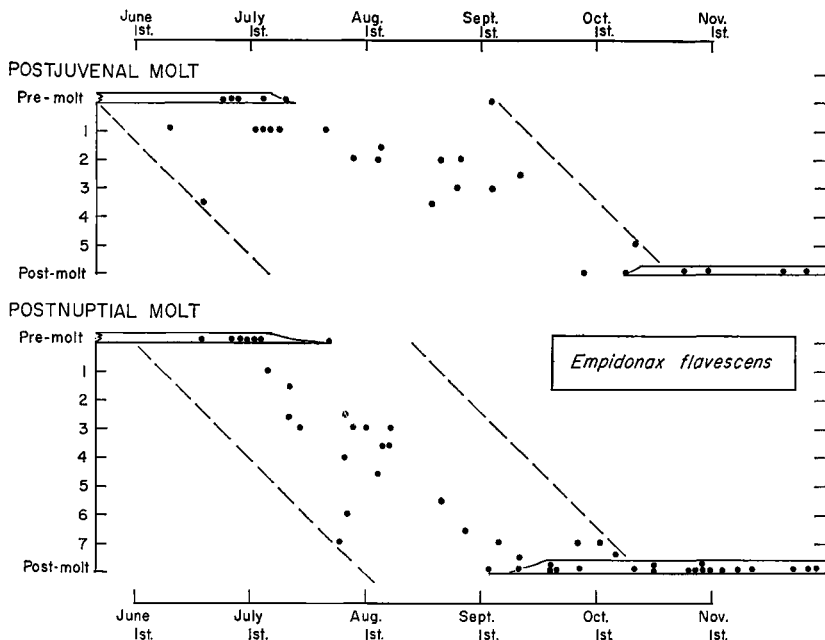*Timing of molt.*—In view of the fact that *E. flavescens* is a species

Figure 2. Timing of postjuvenal and postnuptial molts in *Empidonax flavescens*.

of the subtropical highlands, it is notable that in placement of the post-nuptial molt in the annual cycle the Yellowish Flycatcher shows no great departure from *E. difficilis* of the temperate zone, nor from many other passerines of mid-latitudes. That is, the molt occurs over a period of· several months, immediately following breeding. Such a comparatively confined molt period of *E. flavescens*, even at 10° N in Costa Rica, con-trasts with the relaxed molt and breeding schedules of many species of tropical latitudes. Restricted periods of breeding and molt are considered evidence for temperate zone ancestry of the Yellowish Flycatcher, a point elaborated upon elsewhere.

GEOGRAPHIC VARIATION IN EXTENT OF POSTJUVENAL MOLT

Variation in extent of the postjuvenal molt in the Western Flycatcher and the Yellowish Flycatcher is of interest, especially when examined from a geographic perspective. The essentially linear breeding range of *E. d. difficilis*, from Alaska to northern Baja California, can be divided grossly into northern, central, and southern sections for analysis of extent of postjuvenal molt as revealed by the incomplete plumages of first-year birds taken on their breeding grounds. The much broader

range of *E. d. hellmayri*, from Alberta to Nuevo Leon, can be analyzed in similar fashion (Table 1). The postjuvenal molt is incomplete in all populations of the species; it varies in extent from birds that have replaced only half of the body plumage to those that have replaced all of the body feathers (scattered through all tracts), up to four pairs of inner secondaries, all of the rectrices, and many upper secondary coverts. The north to south decrease in extent of replacement is apparent *within* each form of *E. difficilis* and *between* the races of *E. flavescens*. All populations of *E. d. difficilis* show significantly less extensive postjuvenal molts than all populations of *E. d. hellmayri*.

The direction of the trend is difficult to explain, especially so because it is opposite to those shown in the few other species that have been studied from this standpoint. For example, in several species of wrens of the genus *Campylorhynchus*, southern populations have more extensive postjuvenal molts than northern populations. This may result from the fact that breeding seasons for southern populations are longer and young are produced early. By the time of the postjuvenal molt these young are older than young of northern populations, are presumably more physiologically mature, and hence replace more feathers (Selander 1964). Miller (1933) found that geographic variation in degree of completeness of postjuvenal molt in *Phainopepla nitens* is influenced by date of hatching and possibly by the presence or the absence of migration (although see Phillips et al. 1964). In *Molothrus ater* and *Agelaius phoeniceus*, Selander and Giller (1960) correlated degree of completeness of the postjuvenal molt with age as indicated by degree of cranial ossification.

Pitelka (1951) studied jays in the genus *Aphelocoma* from the standpoint of geographic variation in the timing of the postjuvenal molt and also found that southern populations had more extensive molts than the northern populations. He believed that southern birds existed in more arid and warmer environments than birds to the north and that more extensive postjuvenal molts were adaptive because plumage wear in the arid environments was more severe. Selander (1964) sought similar adaptive relationships between extent of replacement in species of *Campylorhynchus* and their occupancy of warm-arid versus cool-moist regions, but could find no convincing trends.

Races of many of the aforementioned species are sedentary, but even in the Loggerhead Shrike (*Lanius ludovicianus*), in which at least the northern populations are migratory, southern populations have more complete postjuvenal molts than northern populations, and these molts occur on the breeding grounds prior to migration (Miller 1931). Of all the North American species that have been examined for geographic
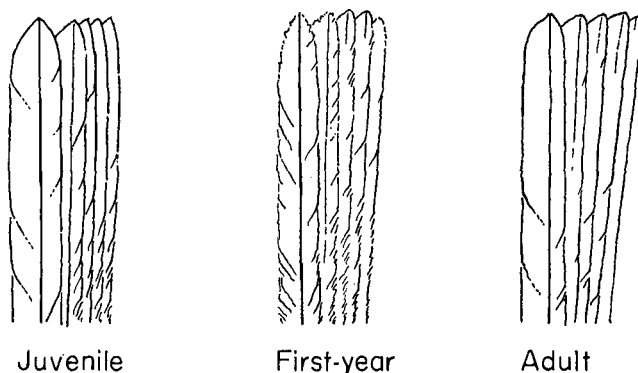
Figure 3.   Dorsal view of rectrices L1 through L5 of three age groups of the Western Flycatcher.

differences in amount of postjuvenal feather replacement, the Western Flycatcher is exceptional in that it molts after migration. Perhaps the reversed trends seen in this species, with northern populations replacing more feathers than southern populations, is somehow related to this fact. However, variation in extent of postjuvenal molt in different populations of the sedentary Yellowish Flycatcher could not be clarified by the invocation of factors related to migration. At present I am unable to explain the interesting geographic trends in postjuvenal molt in either species.

Variation with Age

Age Determination

Since the pioneer work of Miller (1931) on shrikes (*Lanius*), refined research in avian systematics has become increasingly aware of the need for defining and segregating age groups prior to analysis of morphologic variation (Pitelka 1945, Selander 1964, Foster 1967, Selander and Johnston 1967). In *Empidonax* the need for aging criteria is acute; proper identification to species can be impossible unless the general age of the specimen is established beforehand.

As in other *Empidonax* species for which aging criteria have been developed (Johnson 1963a), in *E. difficilis* and *E. flavescens* most juveniles, immatures, and first-year individuals, until midway in the first postnuptial molt, can be distinguished from adults by a combination of the following features: (1) shape of tips of rectrices, which are "pointed" or acuminate in the juvenal generation and more angular or blunt in adults (Figure 3); (2) texture of body plumage, which is fluffier or "looser" and less intensely pigmented in the juvenal generation

TABLE 3

MEASUREMENTS OF AGE GROUPS OF MALES OF *EMPIDONAX DIFFICILIS DIFFICILIS*[1]

Character	Age	No.	Range	Mean ± SE	SD	CV
Primary 10	Adult	14	55.9–59.1	57.41 ± 0.27	1.00	1.74
	First-year	11	53.4–57.6	55.73 ± 0.49	1.63	2.92
Primary 9	Adult	14	62.4–68.9	65.36 ± 0.42	1.56	2.39
	First-year	11	60.4–65.8	63.06 ± 0.53	1.76	2.79
Primary 8	Adult	14	65.1–69.9	66.96 ± 0.35	1.30	1.94
	First-year	11	61.8–67.7	64.57 ± 0.51	1.68	2.60
Primary 7	Adult	14	65.0–69.5	66.68 ± 0.33	1.24	1.86
	First-year	11	63.0–66.4	64.11 ± 0.45	1.51	2.36
Primary 6	Adult	14	62.9–66.6	64.45 ± 0.34	1.29	2.00
	First-year	11	61.0–64.7	62.15 ± 0.39	1.30	2.09
Primary 5	Adult	14	57.9–61.6	59.17 ± 0.24	0.90	1.52
	First-year	10	55.7–60.0	57.56 ± 0.37	1.18	2.05
Primary 4	Adult	14	55.0–58.6	56.18 ± 0.24	0.91	1.62
	First-year	10	53.2–57.1	54.94 ± 0.34	1.09	1.98
Tail	Adult	13	55.8–62.1	58.63 ± 0.48	1.73	2.95
	First-year	11	55.2–61.4	56.69 ± 0.59	1.95	3.44

[1] Sample from the Queen Charlotte Islands, British Columbia.

than in the adults; (3) differential plumage wear, particularly of rectrices and remiges, which in the juvenal generation appear much more frayed near the tips, especially in first-year birds on their breeding grounds, than in the adult generation; and (4) mixed or "patchy" plumage in young versus more "even" plumage in adults, which results from the incompleteness of the postjuvenal molt. For example in a first-year specimen great contrast is often seen between the old pale and worn juvenal wing coverts, secondaries, and rectrices and the comparatively new and bright feathers of those same series that were acquired in the partial postjuvenal molt. The evenness of the adult plumage results from its being comprised of feathers of one generation. Mixed or patchy body plumage of immatures is sometimes difficult to assess because both the adults and young may acquire fresh body feathers in the limited prenuptial molt in the spring. Another criterion which serves as a supplement to the other, more useful, distinguishing features concerns a subtle difference in (5) the luster of the flight feathers. Juvenal feathers seem glossier and adult feathers seem duller under the reflected light of a magnifying lamp, when specimens taken at the same period of the year are compared.

These criteria for determining age apply equally well in either *E. difficilis* or *E. flavescens*. Some individuals of the latter species, however, are more difficult to age properly because occasional immatures have "adult" tails after having replaced all of their rectrices during the post-

TABLE 4

MEASUREMENTS OF AGE GROUPS OF FEMALES OF *EMPIDONAX DIFFICILIS DIFFICILIS*[1]

Character	Age	No.	Range	Mean ± SE	SD	CV
Primary 10	Adult	8	52.8–55.5	53.88 ± 0.32	0.92	1.71
	First-year	7	51.5–53.1	52.34 ± 0.19	0.50	0.96
Primary 9	Adult	8	60.8–62.3	61.60 ± 0.20	0.56	0.91
	First-year	7	58.6–60.6	59.79 ± 0.31	0.83	1.39
Primary 8	Adult	8	62.4–63.9	63.13 ± 0.19	0.54	0.86
	First-year	7	60.4–62.2	61.37 ± 0.27	0.70	1.14
Primary 7	Adult	8	62.1–63.9	63.13 ± 0.24	0.69	1.09
	First-year	7	60.0–62.2	61.31 ± 0.31	0.81	1.32
Primary 6	Adult	8	59.9–61.7	61.06 ± 0.23	0.66	1.08
	First-year	6	58.8–61.3	59.98 ± 0.36	0.89	1.48
Primary 5	Adult	8	55.0–57.5	56.31 ± 0.30	0.84	1.49
	First-year	6	54.3–56.5	55.57 ± 0.33	0.81	1.46
Primary 4	Adult	8	52.4–55.0	53.65 ± 0.29	0.81	1.51
	First-year	6	52.0–54.2	52.85 ± 0.34	0.83	1.57
Tail	Adult	8	54.8–57.5	56.16 ± 0.37	1.04	1.85
	First-year	7	52.4–55.2	53.93 ± 0.39	1.03	1.91

[1] Sample from the Queen Charlotte Islands, British Columbia.

juvenal molt. In these birds the contrast is evident in wear and texture between the new adult rectrices and the slightly more worn juvenal primaries with their paler edges. Further, (6) the buffy edging of the greater and middle secondary coverts differs between subadult and adult birds. These buffy edges on the tips of the coverts are narrower and fluffier in juvenal feathers than in those of adults.

SIZE

As I have stressed previously (Johnson 1963a), an understanding of molt and plumage cycles is fundamentally prerequisite to systematic analysis of species in the genus *Empidonax* because within either sex the inclusive category of juvenile-immature-first-year individuals differs in size from birds 1 year old or older; the latter is the category of "adults" that have undergone at least one complete postnuptial molt.

Sex and age differences in length of primaries 4 through 10 and in length of tail in *E. d. difficilis* from a single sample area (Queen Charlotte Islands, British Columbia) are shown in Tables 3 and 4. Similar data for a sample of males and females of *E. f. flavescens* from Costa Rica are provided in Tables 5 and 6. Mean differences of primary length for sex and age groups of each species are diagrammed in Figures 4 and 5.

In the race *E. d. hellmayri* of the Western Flycatcher sample means of lengths of each of the outer seven primaries of subadults are between 2 and 5% less than sample means of adult males. In females of this race
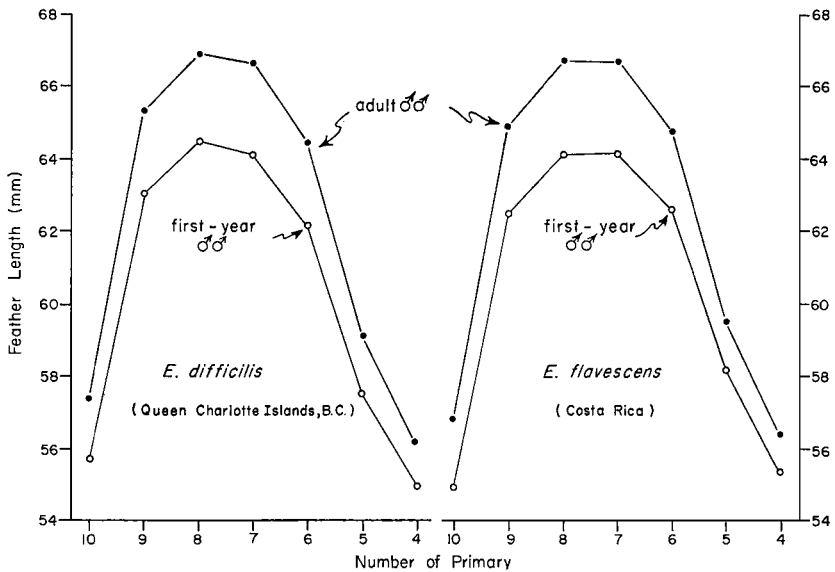
Figure 4. Diagram of wing shapes of adult males and first-year males of Western and Yellowish Flycatchers. Sample means of lengths of each of the outer seven primaries are plotted for each age group of each species. Statistics for these measurements are given in Tables 3 and 5. Note (1) the absolute differences in average feather lengths between subadults and adults within each species, and (2) the difference in wing shape between subadults and adults, which results from a disproportionately greater shortening in first-year birds of primaries 9 through 6 (of the wing tip) versus primary 10 of the leading edge of the wing and primaries 5 and 4 of the trailing edge of the wing.

sample means of comparable wing feather lengths are between 1 and 4% less in subadult versus adult categories. For males of *E. d. difficilis*, wing feather lengths of subadults vary between 1 and 4% shorter than in adults; for females the differences are smaller, the juvenal primaries varying from 0.5 to 3% shorter than those of the adult generation. Rectrices of the juvenal generation in the Western Flycatcher average between 1 and 4% shorter than those of adults, with males and females being rather similar in degree of difference. In *E. flavescens* the size differences observed between subadults and adults are comparable in magnitude to those seen in *E. difficilis*.

CRANIAL PNEUMATIZATION

Details of timing and rates of pneumatization or "ossification" of the skull roof in passerine birds are known for very few species, for example, the House Sparrow, *Passer domesticus* (Nero 1951), Indian Weaver Bird, *Ploceus philippinus* (Biur and Thapliyal 1972), and Zebra Finch,
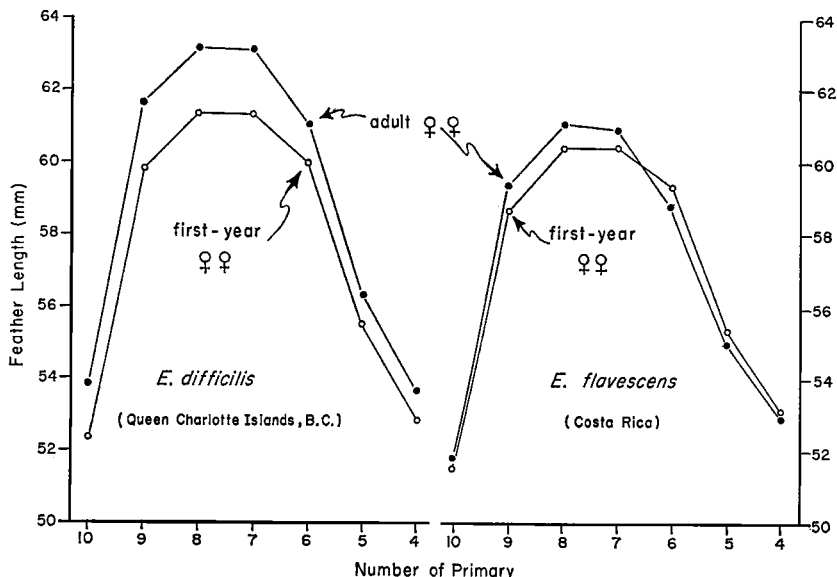
Figure 5. Diagram of wing shapes of adult females and first-year females of Western and Yellowish Flycatchers. Statistics for these measurements are given in Tables 4 and 6. Further explanation is given in the legend to Figure 4. Note the difference in wing shape shown by the sexes when age categories are compared within each species.

Taeniopygia castanotis (Serventy et al. 1967). Although most oscine passeriforms appear to pneumatize the cranium completely within 4 to 8 months after hatching (Harrison and Harrison 1949, Verheyen 1953, Harrison 1964), examples of species with delayed maturation of the skull roof are known (White 1948, Chapin 1949, Bowman 1961, Selander 1964).

Among tyrannids a number of species retain "windows" in the cranium well into the adult period: *Euscarthmornis granadensis, Elaenia obscura, Mionectes striaticollis* (Miller 1963: 32–35), *Myiopagis viridicata* (Grant 1966; although see McNeil 1967), *Myiornis ecaudatus* (McNeil and Martinez 1967), *Empidonax hammondii* (Johnson 1963a: 137), and *Empidonax difficilis* (Johnson 1965: 106–107). Because these "windows" in first-year and adult *Empidonax* seem ossified and rigid, and are apparently not comparable to the flexible and membranous cranial roofs seen in juveniles, I have labeled specimens with crania in this condition as having "first-year skulls." Such an expression suggests the possibility that these rigid yet translucent areas might eventually become fully pneumatized (= double-layered and filled with trabeculae).

TABLE 5

Measurements of Age Groups of Males of *Empidonax flavescens flavescens*[1]

Character	Age	No.	Range	Mean ± SE	SD	CV
Primary 10	Adult	23	54.4–59.2	56.81 ± 0.29	1.35	2.38
	First-year	10	51.8–59.0	54.94 ± 0.73	2.19	3.99
Primary 9	Adult	22	61.6–67.0	64.94 ± 0.28	1.27	1.96
	First-year	10	58.6–67.6	62.56 ± 0.91	2.74	4.38
Primary 8	Adult	22	63.3–69.4	66.76 ± 0.30	1.36	2.04
	First-year	10	60.6–67.8	64.14 ± 0.82	2.47	3.85
Primary 7	Adult	22	63.3–69.3	66.76 ± 0.30	1.36	2.04
	First-year	10	60.7–67.6	64.20 ± 0.80	2.41	3.75
Primary 6	Adult	22	61.8–67.2	64.78 ± 0.31	1.43	2.21
	First-year	10	59.2–66.2	62.68 ± 0.80	2.41	3.84
Primary 5	Adult	22	56.8–61.5	59.55 ± 0.31	1.42	2.38
	First-year	9	54.9–61.0	58.23 ± 0.75	2.12	3.64
Primary 4	Adult	22	53.5–58.5	56.44 ± 0.29	1.34	2.37
	First-year	9	52.4–57.9	55.44 ± 0.69	1.96	3.54
Tail	Adult	25	52.6–57.9	55.24 ± 0.29	1.42	2.57
	First-year	7	49.7–56.5	53.74 ± 0.96	2.35	4.37

[1] Sample from Costa Rica.

Although the pattern and timing of pneumatization of crania in *Empidonax* through the autumn period is poorly known, enough samples of breeding specimens bearing data on degree of skull pneumatization have accumulated during the present study to allow a more precise estimate

TABLE 6

Measurements of Age Groups of Females of *Empidonax flavescens flavescens*[1]

Character	Age	No.	Range	Mean ± SE	SD	CV
Primary 10	Adult	11	48.5–54.4	51.79 ± 0.49	1.55	2.99
	First-year	11	48.8–54.8	51.51 ± 0.59	1.87	3.63
Primary 9	Adult	11	56.5–62.0	59.34 ± 0.57	1.81	3.05
	First-year	11	55.3–61.3	58.64 ± 0.60	1.91	3.26
Primary 8	Adult	11	58.9–63.3	61.05 ± 0.48	1.53	2.51
	First-year	11	56.8–63.3	60.42 ± 0.62	1.98	3.28
Primary 7	Adult	11	59.3–63.2	60.88 ± 0.37	1.16	1.91
	First-year	11	57.1–63.4	60.39 ± 0.62	1.95	3.23
Primary 6	Adult	10	55.9–61.4	58.81 ± 0.50	1.50	2.55
	First-year	10	56.5–62.3	59.33 ± 0.58	1.75	2.95
Primary 5	Adult	10	52.9–57.0	55.02 ± 0.39	1.17	2.13
	First-year	10	53.2–57.7	55.32 ± 0.47	1.42	2.57
Primary 4	Adult	10	51.4–54.2	52.89 ± 0.35	1.06	2.00
	First-year	11	50.6–55.5	53.10 ± 0.43	1.34	2.52
Tail	Adult	17	48.2–53.0	50.94 ± 0.34	1.37	2.69
	First-year	6	48.6–50.2	49.62 ± 0.25	0.55	1.11

[1] Sample from Costa Rica.

TABLE 7

Degree of Cranial Pneumatization in Age Groups of the Western
Flycatcher and the Yellowish Flycatcher[1]

| | Empidonax d. difficilis | | Empidonax d. hellmayri | |
	First-year	Adult	First-year	Adult
Skull "ossified"	3 (20.0%)	8 (27.6%)	0	11 (16.2%)
Skull "windows"	12 (80.0%)	21 (72.4%)	9 (100%)	57 (83.8%)
	Empidonax d. insulicola		Empidonax d. occidentalis	
	First-year	Adult	First-year	Adult
Skull "ossified"	0	0	1 (14.3%)	1 (7.7%)
Skull "windows"	3 (100%)	14 (100%)	6 (85.7%)	12 (92.3%)
	Empidonax f. salvini		Empidonax f. flavescens	
	First-year	Adult	First-year	Adult
Skull "ossified"	1 (100%)	2 (13.3%)	0	1 (7.1%)
Skull "windows"	0	13 (86.7%)	7 (100%)	13 (92.9%)

[1] Based on specimens collected on the breeding grounds. Nomenclature follows a revision of these species (Johnson MS).

of the percentage of both first-year birds and of adults with "unossified" skulls in both *E. difficilis* and *E. flavescens*.

Table 7 provides data on numbers of specimens bearing information on their tags regarding skull condition. These samples have been subdivided further into first-year and adult categories according to plumage criteria considered apart from degree of cranial penumatization. It was important in this tabulation to include only specimens taken by collectors who habitually note the skull condition of *all* specimens they prepare, not just those in which pneumatization is incomplete. The data of Table 7 permit calculation of percentage of breeding specimens with partial pneumatization: 134 of 158 (85%) in *E. difficilis* (races combined) and 33 of 37 (89%) in *E. flavescens* (races combined). These figures can serve as estimates of the percentage of nesting birds in natural populations with incompletely pneumatized crania. The percent difference between each species is probably not significant in view of the small sample for *E. flavescens*. Further, the existence of subspecific difference in average extent of cranial development indicates that these combined figures can serve only as approximations until larger samples of each race are available. Nonetheless, the data suggest that at least 85% of Western and Yellowish Flycatchers on their breeding grounds lack fully pneumatized skulls, an unexpectedly high proportion indeed.

For 64 specimens data are available on relative stage of pneumatization as determined from sketches of crania prepared in the field (Table 8, Figure 6). Importantly, these data throw light on the question of

TABLE 8

FREQUENCY OF BREEDING BIRDS IN EACH STAGE OF PNEUMATIZATION

Form and sample size	I	II	III	IV	V	VI	VII	VIII	Mean stage ± SE
Empidonax d. difficilis[1]									
Adult (15)	—	—	1	3	5	4	1	1	5.27 ± 0.33
First-year (7)	1	2	—	4	—	—	—	—	3.00 ± 0.49
Empidonax d. hellmayri[2]									
Adult (18)	—	—	—	—	6	5	3	4	6.28 ± 0.28
First-year (1)	—	—	—	—	1	—	—	—	5.00
Empidonax d. insulicola[3]									
Adult (14)	1	3	2	5	3	—	—	—	3.43 ± 0.34
First-year ? (1)	1	—	—	—	—	—	—	—	1.00
Empidonax f. salvini (4)[4]									
	—	1	2	1	—	—	—	—	3.00 ± 0.41
Empidonax f. flavescens[5]									
Adult (2)	1	1	—	—	—	—	—	—	1.50 ± 0.50
First-year (2)	1	—	—	1	—	—	—	—	2.50 ± 1.50

[1] Central and northern California.
[2] North central California, eastern Nevada, and New Mexico.
[3] Channel Islands, California.
[4] El Salvador. Data based on skeletons without skins, hence division into first-year and adult categories not possible.
[5] Costa Rica.

whether the patterns of cranial development shown by these two species of flycatchers are retarded or arrested. This is to ask, do skulls of some individuals never pneumatize fully, regardless of the eventual age of the bird? The sample of 22 *E. d. difficilis* shows convincingly that first-year birds have greater average areas of incomplete pneumatization than the adults. A comparison of mean stages reveals the significance of the difference (t-test; $P = 0.001$). Gradual progression of pneumatization with increased age is suggested by the data for *E. d. difficilis* (Table 8); a situation of delayed maturation, rather than one of arrested development, is thus the most suitable explanation. Significantly, all six specimens with fully pneumatized skulls were adult on the basis of plumage criteria. This implies that although some variation in rate of pneumatization is to be expected even among species with generally retarded rates, completion of pneumatization within 1 year may be unlikely if not impossible in the Western Flycatcher.

Data in Table 8 suggest further that *E. d. hellmayri* has a somewhat more advanced rate of pneumatization than does *E. d. difficilis*; mean states of pneumatization in adults of each form are 6.28 versus 5.27, respectively, a difference that is significant ($P < 0.05$). It is of in-
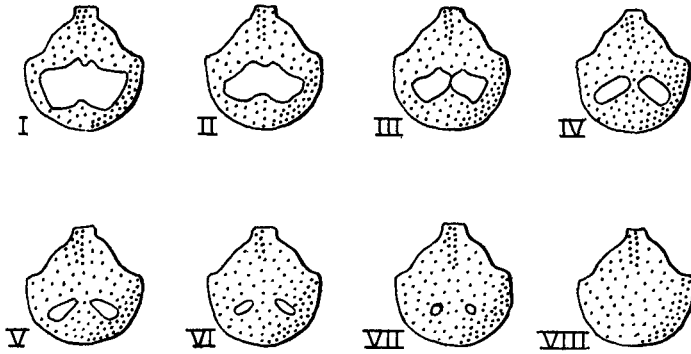
Figure 6. Arbitrary stages of cranial pneumatization in Western and Yellowish Flycatchers. Illustrations were drawn from sketches prepared in the field and are somewhat idealized. Occasional individuals show slight asymmetry of nonpneumatized areas on each side of the skull roof. The edges of the "windows" are sometimes more ragged than indicated.

terest that *E. d. hellmayri* therefore is more advanced than is *E. d. difficilis* both in degree of cranial development and in extent of postjuvenal molt. *E. d. insulicola* is remarkably retarded in average degree of pneumatization, and is highly significantly different ($P < 0.001$) in this regard from *E. d. difficilis* and *E. d. hellmayri*. Grant (1966) exposed a similar situation in insular versus mainland populations of *Myiopagis viridicata*, and one wonders if retarded cranial development is commonplace in island birds. This point is commented upon further in the next section. Note that the eight samples of *E. flavescens* are similar to *E. d. insulicola* in their extreme slowness of cranial pneumatization.

Based on data from *Campylorhynchus*, Selander (1964: 32) predicted that "in passerine birds in general, retarded development of cranial ossification will prove to be associated with delayed recruitment of young into the breeding segment of the population." This prediction is not fulfilled by *Empidonax difficilis*, in which the breeding populations are composed mostly of birds with incompletely pneumatized skulls, birds 1 year of age or older. The same is true for Mexican populations of *Myiopagis viridicata* (Grant 1966), although Venezuelan birds of this species may complete pneumatization earlier (McNeil 1967). A pair of *Myiornis ecaudatus* with cranial "windows" also was breeding (McNeil and Martinez 1967). However the lack of delay in recruitment into breeding populations of these species of tyrannids with partially pneumatized crania does not mean that Selander's prediction is necessarily invalid, because too few species have been examined from this standpoint to enable any broad conclusions.

SIGNIFICANCE OF DELAYED PNEUMATIZATION OF THE CRANIUM

Grant (1966) has reviewed the two main theories offered to explain retention of unpneumatized areas of the skull, that of Harrison and Harrison (1949), who propose adaptive advantages for certain species of swift flight or diving habits that are subject to rapid deceleration, and that of Bowman (1961), who hypothesized adaptive advantages in seed crushing finches through reduction of tension and compression forces in the skull at the time of feeding. In agreement with Selander (1964) I fail to see that any adaptive functional significance in retained cranial "windows" has been demonstrated in any bird. It appears that continued reliance on adaptive functional hypotheses to account for examples of delayed cranial maturation has not led to increased understanding of the phenomenon. Furthermore there are too many exceptions to the explanations mentioned to permit them to serve usefully as bases for research. And, as Grant notes (1966), if functional advantages are conferred by incomplete pneumatization, why do individuals of some species eventually complete the pneumatization process instead of remaining at an arrested state?

A more general hypothesis is needed, one that encompasses the diversity of existing situations. I propose that for passerine birds incomplete pneumatization results not for reasons of adaptive advantage but instead reflects slower rates of general physiologic maturation that obtain in certain species in certain areas. We may note that the species that retain cranial "windows" are commonly of suboscine families of birds, for example, the Tyrannidae, whose lineages are traceable to tropical or subtropical evolutionary centers. Indeed, Miller (1946) believed that doubling of the cranial roof may never be complete in some nonoscine families such as the Furnariidae. Grant (1966) mentions other examples of retarded pneumatization among families of both suboscine and oscine birds in the tropics. Evidence now accumulating from several sources points to the significantly greater survival rates of birds of tropical (Snow 1962, Karr 1971, Ricklefs 1972) versus temperate (Farner 1955) latitudes. These increased survival rates correspond well with the lowered clutch sizes of tropical species that have long been recognized (review in Cody 1971). Birds inhabiting the relatively stable tropics (relatively stable from the standpoint of predictability of resources) may have average longer life spans than species of environments at higher latitudes, which fluctuate more strongly, because increased longevity results from higher rates of survival. Slower rates of maturation are to be expected with increased longevity (Cole 1954), and delayed development of the skull roof may be thought of as but one manifestation of these generally retarded rates. Delayed recruitment of young into breed-

ing populations may also occur in such a setting, thus providing for the possibility predicted by Selander (1964: 32) of a correlation of incomplete pneumatization of the cranium with delayed entry of young into the component of active breeders.

The hypothesis of slower rates of physiologic maturation in more stable environments may also explain instances of delayed development of the skull roof in birds of islands, where maritime environments are typically more uniform than those of the mainland. Retarded rates of skull pneumatization in *Empidonax difficilis insulicola* of the Channel Islands, California (Table 8) and of *Myiopagis viridicata* on the Tres Marías Islands (Grant 1966) versus mainland populations of the same species, and delayed rates of cranial development in the finches of the Galápagos Islands (Bowman 1961) may be cited as examples. Cody (1971: 497–500) provided a useful summary of the similarities of insular and tropical environments, in terms of their relatively uniform climates and predictable resources, and discussed the populational characteristics of birds inhabiting such settings. The notion of delayed rates of physiologic maturation in certain species of both tropical and insular habitats is in keeping with other attributes that seem to be characteristic of populations of such environments, namely decreased reproductive rates and increased survival.

SUMMARY

Based on the examination of 2,100 museum study skins, I analyzed cycles of molt, developed criteria for determining age, and described patterns and rates of skull pneumatization in the Western Flycatcher (*Empidonax difficilis*) and the Yellowish Flycatcher (*Empidonax flavescens*).

In the migratory Western Flycatcher all molts occur on the wintering grounds. The postjuvenal molt varies greatly in extent and takes place between early September and mid-November. Both immatures and adults of this species have a slight prenuptial molt of body plumage between early March and early May. The postnuptial molt of *E. difficilis* is complete and occurs from mid-August to early November. The sedentary Yellowish Flycatcher has only one molt a year. The incomplete postjuvenal molt takes place between June and early October and the first-year birds and adults undergo the complete postnuptial molt between mid-June and early October. The absence of a prenuptial molt in *E. flavescens* is unique in the genus *Empidonax*. Geographic variation is evident in extent of postjuvenal molt in both species, with a north to south decrease in replacement occurring within each race of *E. difficilis* and between the races of *E. flavescens*.

Criteria enabling separation of most specimens of juveniles, immatures, and first-year birds from adults are based on distinctive features of shape, texture, and wear of the juvenal generation of feathers, some of which are retained until the first postnuptial molt. Significant differences in lengths of wing feathers and rectrices between first-year birds and adults require the separation of these age categories prior to systematic analysis.

At least 85% of breeding birds of both species had incompletely pneumatized crania. The data suggest that pneumatization proceeds gradually with age so that some individuals eventually do completely pneumatize the skull roof. I hypothesize that delayed pneumatization of crania in many suboscine birds and in some oscine species of tropical and insular environments is associated with slower rates of general physiologic maturation that may occur in some species of relatively stable or uniform habitats.

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