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MORPHOLOGIC STABILITY VERSUS ADAPTIVE VARIATION IN THE HAMMOND'S FLYCATCHER

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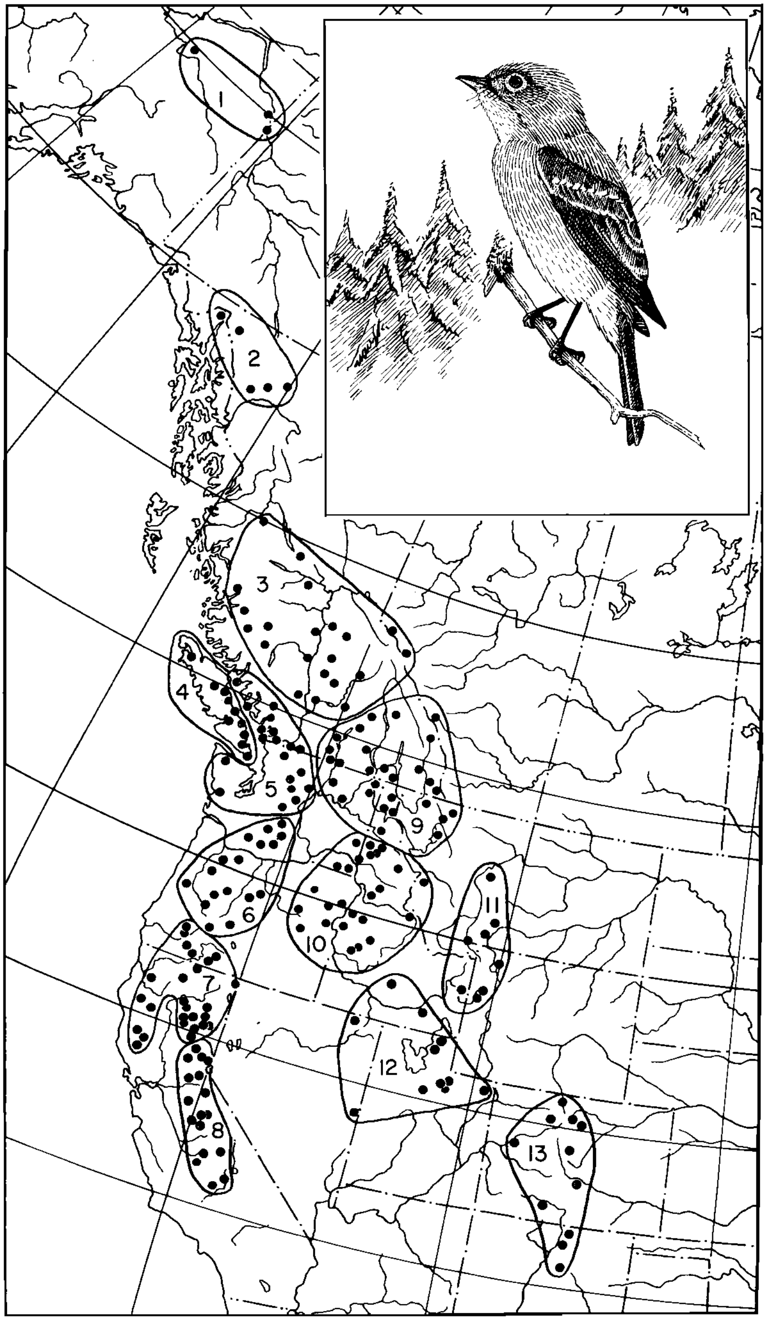
The purpose of this paper is to describe geographic variation in the Hammond's Flycatcher (*Empidonax hammondii*), a species of relatively uniform external morphology despite the fact that it breeds in isolated or semi-isolated populations in boreal regions through 30 degrees of latitude, from central Alaska to northern New Mexico. In an earlier study (Johnson, 1963) I made a gross analysis of size variation in several species of the genus *Empidonax*, including *E. hammondii*, to permit general comparisons between sex-age groups and species for identification purposes. Although that analysis of mixed samples of migrants, summer residents, and wintering birds revealed no evidence of significant geographic variation in the Hammond's Flycatcher, a more refined approach, made possible by the availability of more abundant material, was necessary for the following reasons. (1) The reliability of certain previously presented criteria of identification needed to be tested. (2) Subtle patterns of variation needed to be explored to determine if they could provide evidence to support the suggestion (Johnson, 1963: 214) that the Hammond's Flycatcher and the Least Flycatcher (*Empidonax minimus*) diverged from a common ancestor. (3) Jewett *et al.* (1953: 427) suggested racial division of *E. hammondii* on the basis of color; possible concordant variation in size needed to be investigated. (4) Information on bill width, bill depth, tarsal length plus middle toe length, and body weight had not been offered previously.

On general grounds such an investigation is worthwhile also because studies of variation within species of birds that show no striking size divergence are seldom undertaken, a fact which erroneously implies that variation below the "subspecific level of recognition" is meaningless or nonexistent. Furthermore, such data are useful to ecologists who need fundamental detailed information on geographic variation in size (e.g., Hespenheide, 1964) when speculating on the role of competition in the promotion of niche divergence and morphologic discontinuities.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ANALYSIS OF VARIATION

This study is based on data obtained from 545 specimens of summer resident Hammond's Flycatchers. Approximately 150 of these skins were unavailable at the time of my earlier description of general variation within the species. These specimens were from breeding localities and have been aged according to criteria outlined previously (Johnson, 1963: 136–140). The localities from which specimens were examined have been grouped for treatment into 13 sample areas or populations (Figure 1). These areas have been delineated so as to permit gross comparison of the major biogeographic regions occupied by this species (Sierra Nevada Mountains versus Southern Rocky Mountains and Northern Cascade Mountains versus Vancouver Island, as examples). The unfortunate expanse of several of the population areas (such as number 12), while perhaps masking numerous intrapopulational trends, was necessary so that samples large enough for meaningful statistical analysis could be assembled. As will be apparent from the tables, specimens are scarce north of population 3, through western Canada and Alaska. Treatment of variation in that region is thus tentative and relatively superficial.

Measurements.—Various measurements were taken as follows: the length of the tenth primary, as the chord, from the bend of the wing to the tip of that feather; tail length, from a point on the skin between the insertions of the central rectrices (1–1) to the tip of the longest rectrix; bill length, from the anterior margin of the nostril to the bill tip; bill depth, from the culmen to the lower edges of the rami; bill width, from one tomium to the other (both bill depth and width were taken where a plane drawn at right angles to the bill passes through the anterior margin of the nostril); length of the tarsus, as the diagonal from the mid-point of the posterior surface juncture of the tibia and the metatarsus to the anterior lower edge of the scute (usually the lowest undivided scute) opposite the insertion of the proximal part of the base of the hind toe; middle toe without claw, as the diagonal from the anterior lower edge of the same lowest undivided scute to the tip of the toe pad on the ventral surface of the toe. Because of apparent variation in the position of the lowest undivided scute and because of doubts that the lowest undivided scute was always the same scute in the series of specimens, the measurements of tarsal length and middle toe length were summed before analysis. The use of the same reference scute for both measurements presumably insured uniformity of treatment. Linear measurements are in millimeters; weights are in grams.

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Figure 1. Breeding distribution of the Hammond's Flycatcher in western North America. Each dot represents the locality of collection for one or more specimens examined in this study. Populations analyzed are numbered.

TABLE 1

LENGTH, IN MILLIMETERS, OF THE TENTH PRIMARY IN THE HAMMOND'S FLYCATCHER[1]

Population[2] *Number*	*Age*	Males					Females				
		Sample size	*Range*	*Mean and standard error*[3]	*S. D.*[3]	*C. V.*[3]	*Sample size*	*Range*	*Mean and standard error*[3]	*S. D.*[3]	*C. V.*[3]
1	Adult	6	61.8–64.0	63.17	—	—	—	—	—	—	—
	First-year	—	—	—	—	—	1	55.7	—	—	—
2	Adult	6	58.3–63.0	61.12	—	—	4	56.5–58.2	57.32	—	—
	First-year	3	59.7–61.1	60.63	—	—	—	—	—	—	—
3	Adult	41	57.2–65.9	61.70 ± 0.32	2.06	3.35	20	53.6–60.4	57.06 ± 0.43	1.93	3.38
	First-year	23	55.4–63.6	60.33 ± 0.42	2.03	3.36	7	54.9–59.7	56.66	—	—
4	Adult	18	60.0–66.7	62.20 ± 0.40	1.71	2.74	12	54.8–60.4	57.60 ± 0.43	1.48	2.56
	First-year	10	58.2–63.5	60.92 ± 0.50	1.60	2.62	5	55.2–57.5	56.46	—	—
5	Adult	15	60.6–63.8	62.07 ± 0.30	1.16	1.86	5	57.0–59.1	58.04	—	—
	First-year	10	59.0–63.4	61.17 ± 0.43	1.36	2.22	6	56.2–59.3	56.90	—	—
6	Adult	10	60.3–64.2	61.57 ± 0.36	1.15	1.87	1	57.0	—	—	—
	First-year	8	56.8–63.6	61.49	—	—	4	55.7–58.5	56.82	—	—
7	Adult	32	60.5–65.1	62.93 ± 0.24	1.35	2.14	11	52.1–58.2	56.76 ± 0.52	1.73	3.05
	First-year	16	59.6–63.6	61.77 ± 0.23	0.93	1.50	11	55.0–59.8	57.02 ± 0.43	1.43	2.50
8	Adult	12	57.8–65.2	61.54 ± 0.70	2.42	3.93	7	54.8–59.2	56.77	—	—
	First-year	14	58.8–64.7	61.31 ± 0.41	1.54	2.51	8	55.7–59.2	57.54	—	—
9	Adult	42	59.7–66.5	62.58 ± 0.22	1.45	2.32	24	54.3–60.3	57.85 ± 0.28	1.39	2.40
	First-year	17	59.3–65.4	61.42 ± 0.35	1.45	2.36	1	56.0	—	—	—
10	Adult	30	58.3–65.3	62.25 ± 0.27	1.48	2.38	8	55.7–59.4	57.81	—	—
	First-year	16	60.4–63.3	61.94 ± 0.24	0.95	1.54	13	54.5–61.7	58.03 ± 0.53	1.90	3.28
11	Adult	7	60.3–64.5	62.38	—	—	3	56.9–58.3	57.57	—	—
	First-year	3	61.7–62.7	62.20	—	—	1	58.4	—	—	—
12	Adult	12	60.9–64.2	62.48 ± 0.32	1.12	1.80	2	57.5–58.1	57.80	—	—
	First-year	5	60.4–64.3	62.42	—	—	4	56.5–59.5	58.28	—	—
13	Adult	15	61.4–65.9	63.56 ± 0.39	1.51	2.37	9	56.4–60.4	58.09	—	—
	First-year	4	61.3–63.0	62.35	—	—	3	56.4–58.1	57.27	—	—
Entire species sample	Adult	246	57.2–66.7	62.31 ± 0.11	1.67	2.68	106	52.1–60.4	57.50 ± 0.15	1.52	2.64
	First-year	129	55.4–65.4	61.33 ± 0.12	1.31	2.14	64	54.5–61.7	57.26 ± 0.19	1.52	2.65

[1] See Figure 2 for graphic comparison of these samples for males.

[2] See Figure 1 for the locations of populations.

[3] Not calculated for samples of fewer than 10 individuals.

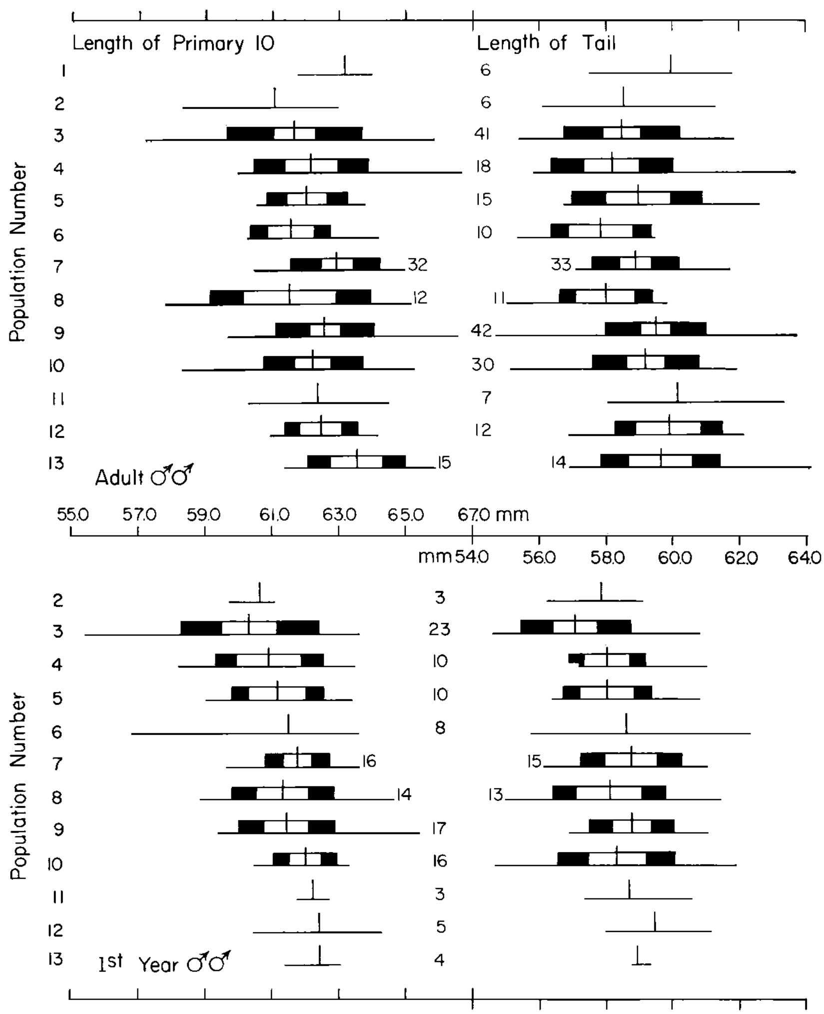

Figure 2. Statistical analysis of length of the tenth primary (left) and length of tail (right) in adult (upper) and first-year (lower) male Hammond's Flycatchers. Population numbers refer to areas shown in Figure 1. The horizontal line of each figure indicates the sample range. Vertical line indicates sample mean. Black rectangle represents one standard deviation on each side of mean; white rectangle represents two standard errors on each side of mean. Sample sizes are indicated near each figure.

In the following section, positive statements on statistical significance of differences are based on the non-overlap of two standard errors of the means of each of two populations. In each case significance of differences

TABLE 2
TAIL LENGTH, IN MILLIMETERS, OF THE HAMMOND'S FLYCATCHERS[1]

Population number[2]	*Age*	*Males*					*Females*				
		Sample size	*Range*	*Mean and standard error*[3]	*S. D.*[3]	*C. V.*[3]	*Sample size*	*Range*	*Mean and standard error*[3]	*S. D.*[3]	*C. V.*[3]
1	Adult	6	57.5–61.8	59.97	—	—	—	—	—	—	—
	First-year	—	—	—	—	—	1	54.9	—	—	—
2	Adult	6	56.1–61.3	58.53	—	—	4	54.8–56.3	55.62	—	—
	First-year	3	56.2–59.1	57.83	—	—	—	—	—	—	—
3	Adult	41	55.4–61.9	58.51 ± 0.27	1.75	2.98	20	52.5–58.1	54.98 ± 0.32	1.43	2.61
	First-year	23	54.6–60.8	57.07 ± 0.35	1.66	2.91	7	52.5–61.0	54.64	—	—
4	Adult	18	55.8–63.7	58.19 ± 0.43	1.83	3.14	12	51.5–56.6	54.46 ± 0.45	1.56	2.86
	First-year	10	57.2–61.0	58.01 ± 0.36	1.14	1.97	5	53.0–55.1	54.08	—	—
5	Adult	15	56.8–62.6	58.93 ± 0.48	1.88	3.18	5	54.3–55.2	54.66	—	—
	First-year	10	56.3–60.8	58.01 ± 0.42	1.33	2.30	6	52.5–56.5	54.17	—	—
6	Adult	10	55.3–59.4	57.85 ± 0.48	1.51	2.62	1	57.0	—	—	—
	First-year	8	55.7–62.3	58.59	—	—	4	52.7–56.2	54.10	—	—
7	Adult	33	57.1–61.7	58.91 ± 0.23	1.30	2.20	11	52.1–57.6	55.44 ± 0.50	1.65	2.98
	First-year	15	56.1–61.0	58.73 ± 0.38	1.48	2.53	11	52.9–56.5	54.81 ± 0.33	1.08	1.98
8	Adult	11	55.0–59.8	58.04 ± 0.44	1.45	2.50	7	52.6–57.9	55.14	—	—
	First-year	13	54.9–61.4	58.07 ± 0.49	1.77	3.04	8	52.5–56.2	54.41	—	—
9	Adult	42	54.7–63.7	59.47 ± 0.23	1.52	2.56	24	53.0–58.5	55.63 ± 0.30	1.45	2.61
	First-year	17	56.9–61.0	58.74 ± 0.30	1.23	2.10	1	54.6	—	—	—
10	Adult	30	55.1–61.9	59.19 ± 0.29	1.58	2.67	8	54.8–58.6	56.76	—	—
	First-year	16	54.6–61.9	58.31 ± 0.44	1.75	3.01	13	53.8–60.2	56.77 ± 0.55	1.98	3.49
11	Adult	7	58.1–63.3	60.17	—	—	3	55.6–56.0	55.87	—	—
	First-year	3	57.3–60.5	58.63	—	—	1	56.5	—	—	—
12	Adult	12	56.9–62.1	59.90 ± 0.48	1.66	2.78	2	53.0–56.6	54.80	—	—
	First-year	5	57.9–61.1	59.42	—	—	4	56.2–56.6	56.42	—	—
13	Adult	14	56.9–64.1	59.64 ± 0.47	1.78	2.98	9	53.6–57.5	55.44	—	—
	First-year	4	58.7–59.3	58.90	—	—	3	54.6–56.2	55.63	—	—
Entire species sample	Adult	245	54.7–64.1	58.98 ± 0.11	1.70	2.88	106	51.5–58.6	55.35 ± 0.14	1.47	2.66
	First-year	127	54.6–62.3	58.20 ± 0.15	1.63	2.80	64	52.5–61.0	55.10 ± 0.23	1.82	3.30

[1] See Figure 2 for graphic comparison of these samples for males.
[2] See Figure 1 for the locations of populations.
[3] Not calculated for samples of fewer than 10 individuals.

established on this basis were verified at the 95 per cent level by the use of the "*t*" test.

Length of the tenth primary.—This primary is significantly longer in the adult males (Table 1, Figure 2) of populations 7 and 13 than in those of populations 3 and 6; otherwise there is great uniformity. Among samples of first-year males, those from population 7 are longer than those from area 3. Although there are only four birds available from sample area 13, they are all relatively long-winged; a larger sample would probably show that first-year birds from this area are significantly longer in the length of the tenth primary than those from, at least, area 3. Among the samples of females (Table 1) there are no significant differences between populations of either adults or first-year birds. Samples of females are small, however, particularly for the younger birds.

Tail length.—Adult males (Table 2, Figure 2) from population 9 have significantly longer tails than those from sample areas 4, 6, and 8. Surprisingly, among the first-year males, those from populations 7 and 9 are longer than 3; hence, the variation of these younger males does not follow the pattern seen among the adults. In the adult females (Table 2) no significant differences were found in tail length between any of the populations. In contrast, first-year females from population 10 are significantly longer-tailed than those from sample 7. Other samples of first-year females are too small for a revealing statistical treatment.

Bill length.—Except for population 4 (Vancouver Island), the males of which average significantly longer in bill length than adjacent populations 3 and 5, interpopulational differences are minor. A weak clinal increase in bill length is found from British Columbia to the Sierra Nevada of California (Table 3, Figure 3). Although population 3 at one end of the series is significantly smaller than populations 7 and 8 at the other end, these extremes are connected by a series of populations that average intermediate in size. Bill lengths of males in population 3 are also significantly shorter than those in adjacent population 9 to the southeast, but are similar in size to other more distant populations in the Rocky Mountains. Among females (Table 3) no such patterns are evident. Females from population 9 are significantly smaller than those from populations 4, 5, and 8; otherwise bill length seems to be very uniform in this sex. Therefore, the present samples, at least, demonstrate the lack of striking changes in bill length of females, although statistically significant differences exist between means of several samples. Differences between other populations could probably be demonstrated if more birds were available for certain samples.

Bill depth.—In bill depth, both males (Table 3, Figure 3) and females show great uniformity in all populations.

TABLE 3
BILL LENGTH AND DEPTH, IN MILLIMETERS, IN THE HAMMOND'S FLYCATCHER[1]

Population[2] number	Sex	Bill length					Bill depth				
		Sample size	Range	Mean and standard error[3]	S. D.[3]	C. V.[3]	Sample size	Range	Mean and standard error[3]	S. D.[3]	C. V.[3]
1	Male	5	6.8–7.4	7.08	—	—	2	3.0–3.3	3.15	—	—
	Female	1	6.2	—	—	—	1	3.4	—	—	—
2	Male	9	6.5–7.7	7.04	—	—	7	3.1–3.3	3.23	—	—
	Female	4	6.2–6.7	6.52	—	—	3	3.0–3.1	3.03	—	—
3	Male	61	6.3–7.7	7.02 ± 0.04	0.33	4.67	46	2.8–3.5	3.16 ± 0.03	0.17	5.54
	Female	26	6.4–7.8	6.97 ± 0.06	0.32	4.56	20	2.9–3.8	3.21 ± 0.04	0.20	6.14
4	Male	28	6.8–8.2	7.37 ± 0.06	0.35	4.69	18	3.0–3.4	3.20 ± 0.03	0.13	4.00
	Female	17	6.7–7.5	7.12 ± 0.07	0.28	3.95	13	3.0–3.5	3.20 ± 0.04	0.15	4.59
5	Male	25	6.5–7.6	7.11 ± 0.06	0.31	4.43	18	2.9–3.5	3.25 ± 0.04	0.15	4.65
	Female	11	6.7–7.4	7.06 ± 0.06	0.22	3.07	8	2.8–3.6	3.25	—	—
6	Male	18	6.8–7.5	7.13 ± 0.05	0.21	2.93	10	3.1–3.5	3.24 ± 0.04	0.13	4.10
	Female	5	6.1–7.6	6.94	—	—	4	3.0–3.3	3.15	—	—
7	Male	46	6.6–7.9	7.21 ± 0.05	0.32	4.38	40	2.9–3.5	3.18 ± 0.02	0.14	4.40
	Female	22	6.3–7.5	6.99 ± 0.07	0.34	4.88	20	2.9–3.4	3.12 ± 0.03	0.12	3.94
8	Male	26	6.4–8.9	7.30 ± 0.10	0.53	7.30	23	2.9–3.5	3.15 ± 0.04	0.18	5.81
	Female	15	6.7–7.8	7.11 ± 0.09	0.33	4.66	13	2.9–3.3	3.16 ± 0.03	0.12	3.76
9	Male	54	6.6–8.6	7.25 ± 0.05	0.37	5.06	37	2.8–3.6	3.20 ± 0.03	0.17	5.25
	Female	23	5.7–7.6	6.74 ± 0.10	0.49	7.24	16	2.9–3.4	3.11 ± 0.04	0.14	4.47
10	Male	45	6.2–7.8	7.14 ± 0.05	0.34	4.82	26	2.9–3.6	3.18 ± 0.03	0.17	5.38
	Female	20	6.3–7.6	6.87 ± 0.08	0.38	5.46	13	2.8–3.3	3.10 ± 0.04	0.15	4.94
11	Male	10	6.5–7.8	7.14 ± 0.15	0.47	6.54	8	3.0–3.4	3.18	—	—
	Female	4	6.9–7.2	7.05	—	—	3	3.1–3.2	3.13	—	—
12	Male	15	6.6–7.9	7.25 ± 0.11	0.42	5.81	13	2.9–3.5	3.13 ± 0.05	0.18	5.75
	Female	6	6.4–7.4	6.90	—	—	6	2.8–3.3	3.12	—	—
13	Male	18	6.4–7.6	7.07 ± 0.06	0.28	3.90	14	3.0–3.4	3.14 ± 0.04	0.14	4.49
	Female	12	6.5–7.6	6.85 ± 0.10	0.34	4.92	11	2.9–3.5	3.16 ± 0.05	0.16	5.00
Entire species sample	Male	360	6.2–8.9	7.17 ± 0.02	0.37	5.09	262	2.8–3.6	3.18 ± 0.01	0.18	5.63
	Female	166	6.1–7.8	6.94 ± 0.03	0.37	5.36	131	2.8–3.8	3.15 ± 0.01	0.16	5.11

[1] Adult and first-year individuals combined within each sex. See Figure 3 for graphic presentation of these measurements for males.
[2] See Figure 1 for locations of populations.
[3] Not calculated for samples of fewer than 10 individuals.

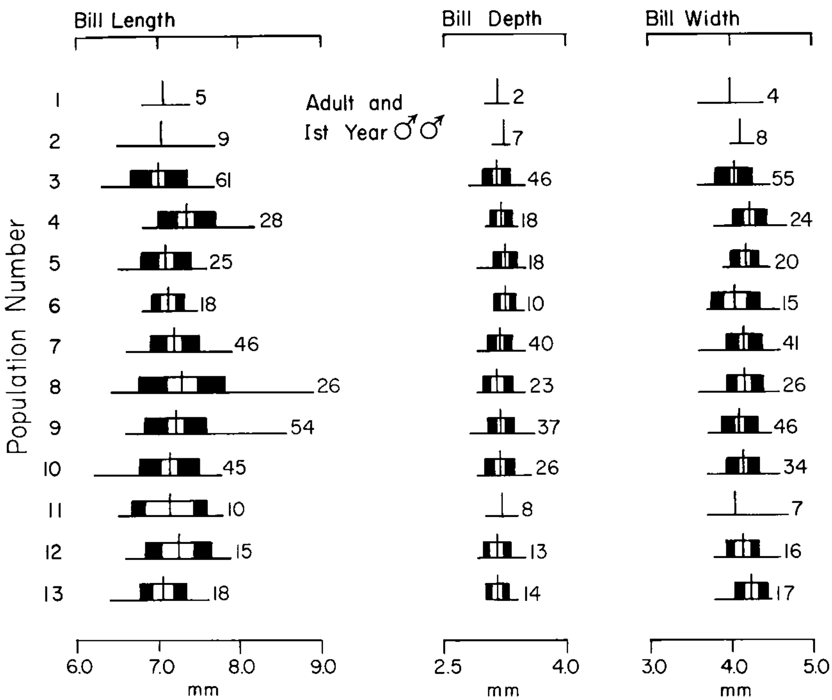

Figure 3. Statistical analysis of bill measurements of male Hammond's Flycatchers. See legend to Figure 2 for explanation of symbols.

Bill width.—In this character (Table 4, Figure 3) males from population 3 have significantly narrower bills than those from adjacent populations 4 and 5. The latter two populations are not different, however. The differences between population 3, and 7 or 8, are significant at the 95 per cent level, indicating a trend toward increased size in the southern Cascades and Sierra Nevada. In this character the females show no significant differences between populations.

Tarsal length plus length of middle toe.—In this character male birds (Table 4, Figure 4) from populations 3, 8, and 13 are significantly smaller than those from population 5. The sample from population 8 is also significantly smaller than birds from population 4, as well as adjacent populations 7 and 9. All of the samples of females show great uniformity; none appears to differ at any significant level.

Body weight.—Only three samples of males (Table 5, Figure 4) are large enough for statistical treatment. Of these, birds from population 8 are significantly lighter than those from area 3, and from adjacent popula-

TABLE 4

BILL WIDTH AND LENGTH OF THE MIDDLE TOE PLUS TARSUS, IN MILLIMETERS, OF THE HAMMOND'S FLYCATCHER[1]

Population[2] number	*Sex*	Bill width					Length of middle toe plus tarsus				
		Sample size	*Range*	*Mean and standard error[3]*	*S. D.[3]*	*C. V.[3]*	*Sample size*	*Range*	*Mean and standard error[3]*	*S. D.[3]*	*C. V.[3]*
1	Male	4	3.6–4.4	4.00	—	—	3	24.3–25.1	24.63	—	—
	Female	1	3.9	—	—	—	1	24.0	—	—	—
2	Male	8	4.0–4.3	4.14	—	—	9	24.0–25.8	24.82	—	—
	Female	3	3.5–4.1	3.87	—	—	4	23.7–25.1	24.55	—	—
3	Male	55	3.6–4.5	4.05 ± 0.03	0.22	5.53	63	23.2–27.3	24.64 ± 0.10	0.78	3.14
	Female	23	3.9–4.6	4.13 ± 0.04	0.17	4.21	27	22.3–25.7	24.02 ± 0.17	0.86	3.57
4	Male	24	3.8–4.7	4.23 ± 0.05	0.22	5.20	27	23.6–26.1	24.88 ± 0.13	0.70	2.80
	Female	15	3.8–4.8	4.27 ± 0.06	0.24	5.62	17	23.2–26.8	24.27 ± 0.20	0.82	3.37
5	Male	20	3.9–4.5	4.18 ± 0.04	0.17	4.02	23	24.0–26.3	25.07 ± 0.12	0.57	2.26
	Female	9	3.8–4.3	4.14	—	—	11	23.2–25.0	24.14 ± 0.16	0.53	2.20
6	Male	15	3.7–4.6	4.07 ± 0.07	0.28	6.93	17	23.4–25.9	24.68 ± 0.18	0.72	2.92
	Female	5	4.0–4.5	4.30	—	—	5	23.5–25.4	24.32	—	—
7	Male	41	3.6–4.6	4.16 ± 0.04	0.22	5.34	47	22.9–26.5	24.84 ± 0.12	0.80	3.22
	Female	20	3.6–4.5	4.24 ± 0.05	0.20	4.81	22	22.3–26.4	23.96 ± 0.18	0.82	3.43
8	Male	26	3.6–4.6	4.18 ± 0.04	0.22	5.24	25	22.6–25.8	24.36 ± 0.15	0.74	3.05
	Female	13	3.9–4.8	4.30 ± 0.06	0.23	5.44	14	23.1–25.2	24.08 ± 0.20	0.76	3.14
9	Male	46	3.7–4.5	4.10 ± 0.03	0.22	5.36	56	23.2–27.0	24.90 ± 0.12	0.88	3.52
	Female	18	3.7–4.4	4.17 ± 0.05	0.22	5.32	25	22.7–26.3	24.27 ± 0.15	0.77	3.17
10	Male	34	3.7–4.6	4.15 ± 0.03	0.20	4.75	44	23.2–26.8	24.98 ± 0.12	0.80	3.21
	Female	15	3.7–4.4	4.14 ± 0.06	0.22	5.31	21	23.1–25.7	24.45 ± 0.15	0.70	2.85
11	Male	7	3.7–4.7	4.06	—	—	10	24.0–26.1	24.82 ± 0.22	0.69	2.79
	Female	3	3.8–4.3	4.13	—	—	4	23.9–24.9	24.35	—	—
12	Male	16	3.8–4.6	4.14 ± 0.05	0.20	4.76	17	23.0–28.0	24.80 ± 0.28	1.15	4.62
	Female	6	4.0–4.4	4.15	—	—	6	22.6–25.5	24.30	—	—
13	Male	17	3.8–4.5	4.25 ± 0.05	0.19	4.47	18	22.6–25.7	24.46 ± 0.17	0.71	2.88
	Female	11	4.0–4.3	4.17 ± 0.04	0.13	3.02	11	23.0–25.6	24.11 ± 0.21	0.70	2.90
Entire species sample	Male	313	3.6–4.7	4.13 ± 0.02	0.21	5.08	359	22.6–28.0	24.78 ± 0.04	0.79	3.19
	Female	142	3.5–4.8	4.18 ± 0.02	0.22	5.24	168	22.3–26.8	24.19 ± 0.06	0.76	3.15

[1] Adult and first-year individuals combined within each sex. See Figures 3 and 4 for graphic presentation of these measurements.

[2] See Figure 1 for locations of populations.

[3] Not calculated for samples of fewer than 10 individuals.

tion 7. The 5 females from sample area 8 are also relatively light when compared with the 19 birds from area 7. Weights of females are generally too few to enable meaningful discussion of the variation of this character in that sex.

SEXUAL DIMORPHISM

Percentage of sexual dimorphism in size is calculated by dividing the difference between the mean measurements of males and females (Tables 1–5) by the mean for males: [(M♂♂–M♀♀)/M♂♂].

In length of the tenth primary males average from 6 to 10 per cent greater than females (Figure 5); uniformity in degree of dimorphism in this character from one population to another is therefore impressive. Sexual dimorphism in size among first-year birds is usually slightly less than among adults. For comparative purposes, the mean percentages of dimorphism of both length of the tenth primary and the length of the tail both for adult and first-year Least Flycatchers, a supposed close relative of the Hammond's Flycatcher, are also plotted in Figure 5. These values were obtained from mixed samples of the species from many parts of the range; they have no relationship to populations 6 and 7 of *E. hammondii*, near which they are plotted.

The span of interpopulational variation in degree of sexual dimorphism in tail length is comparable to that shown by the length of the tenth primary in that males are from 3 to 7 per cent greater than females. First-year birds are very similar to adults in amount of dimorphism in this character where samples of meaningful size are available for both age groups.

Sexual dimorphism in body weight shows strong interpopulational differences for the three samples of fair size (Figure 5), differences that are discordant with the length of the tenth primary and with tail length. Thus, males from population 3 average seven per cent heavier than females, although in population 7 there is apparently no sexual dimorphism in body weight, and in population 8 it amounts to less than two per cent. More weight data from all sample areas are badly needed.

In tarsal length plus length of middle toe, sexual dimorphism is moderate and rather uniform; males average from one to four per cent longer than females.

Variation is impressive within each of the three dimensions of the bill that were measured (Figure 5). Sexual dimorphism in bill length, for example, varies from less than one per cent to seven per cent, with males always larger than females. Even adjacent populations, such as number 3 and number 9, may show extreme differences in amout of dimporhism of this character. Dimorphism in bill depth seems somewhat less pro-

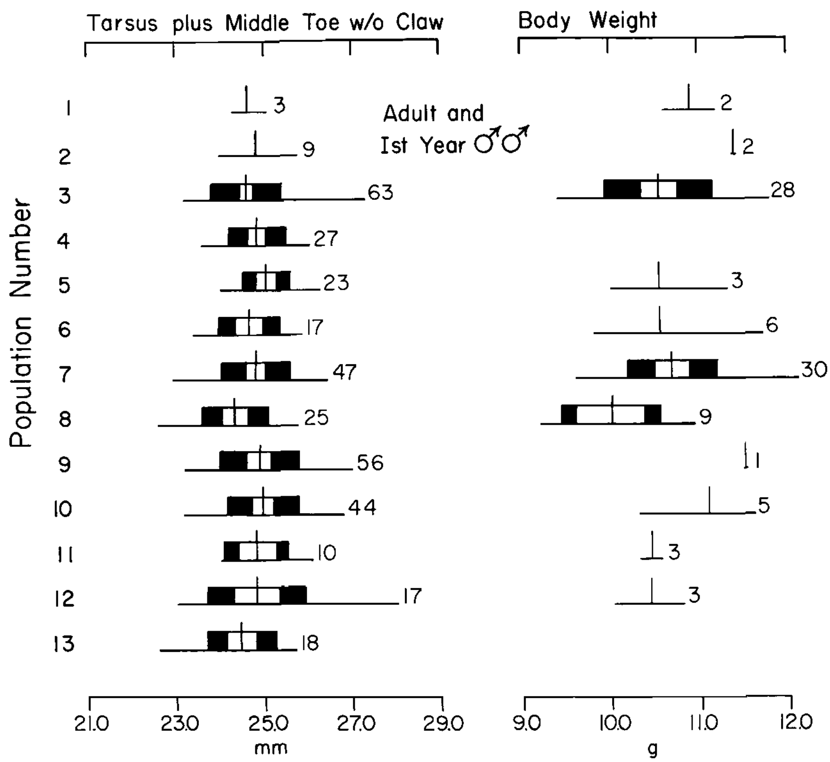

Figure 4. Statistical analysis of measurements of length of the tarsus plus middle toe and of body weight in male Hammond's Flycatchers. See legend to Figure 2 for explanation of symbols.

nounced. Except for the small sample for population 2, which suggests that bills of males average approximately six per cent deeper than bills of females, bills of males from no other population average over three per cent deeper than females. In several samples (numbers 3, 4, 5, 8, and 13) males are either identical to the females in depth of bill or the bills of females are actually up to two per cent deeper than males. Unexpectedly, in many of the populations the females have wider bills than the males, ranging from one to six per cent (population 6) wider. There is much variation, however, for in populations 10 and 12 the sexes are similar in bill width, although in populations 2, 5, and 13, the males have wider bills by as much as six per cent.

Such descriptions as are offered above of interpopulational differences in degree of dimorphism of a single dimension of the bill obscure one of the most interesting patterns of variation brought out in the present study,

TABLE 5
BODY WEIGHT, IN GRAMS, OF THE HAMMOND'S FLYCATCHER[1]

Population[2] *number*	*Sex*	*Sample size*	*Range*	*Mean and standard error*[3]	*S. D.*[3]	*C. V.*[3]
1	Male	2	10.6–11.2	10.90	—	—
2	Male	2	11.4	11.40	—	—
	Female	2	10.5–12.0	11.25	—	—
3	Male	28	9.4–11.8	10.56 ± 0.11	0.59	5.60
	Female	5	8.8–10.3	9.80	—	—
5	Male	3	10.0–11.3	10.53	—	—
6	Male	6	9.8–11.7	10.57	—	—
	Female	1	9.5	—	—	—
7	Male	30	9.6–12.1	10.68 ± 0.09	0.50	4.72
	Female	19	9.5–12.9	10.72 ± 0.22	0.97	9.08
8	Male	9	9.2–10.9	9.99 ± 0.19	0.56	5.60
	Female	5	9.1–10.7	9.80	—	—
9	Male	1	11.5	—	—	—
	Female	4	9.4–10.2	9.80	—	—
10	Male	5	10.3–11.6	11.08	—	—
	Female	4	8.0–11.5	10.02	—	—
11	Male	3	10.3–10.6	10.43	—	—
12	Male	3	10.0–10.8	10.43	—	—
	Female	3	10.0–10.1	10.03	—	—
Entire species sample	Male	91	9.2–12.1	10.59 ± 0.06	0.58	5.43
	Female	44	8.0–12.9	10.30 ± 0.14	0.94	9.10

[1] Adult and first-year birds combined within each sex. See Figure 4 for graphic presentation of these weights for males.
[2] See Figure 1 for locations of populations.
[3] Not calculated for samples of fewer than 10 individuals.

namely that *intra*populational comparisons of dimorphism in all bill dimensions indicate divergence in bill *shape* between the sexes. Only populations 2 and 5 do not fit this generalization. In population 2 (small sample) the bills of males seem to be uniformly larger than females by approximately six or seven per cent. Population 5 is apparently sexually monomorphic in all bill dimensions. In other populations, however, there may be no dimorphism in one feature of the bill, but moderate dimorphism in other dimensions (examples are populations 3 and 4), leading to differences in bill shape. A striking example of difference in bill shape between males and females is shown by population 6 in which the males average approximately three per cent greater than females in both bill length and bill depth, while in bill width the males average approximately six per cent narrower than females.

Because the great differences in sexual dimorphism in the Hammond's Flycatcher mainly concern the bill, the principal or sole food gathering tool, I speculate that the differences in bill shape between males and females are adaptive in that they function to reduce intraspecific competition for food. The most critical stage for reduction of such competition

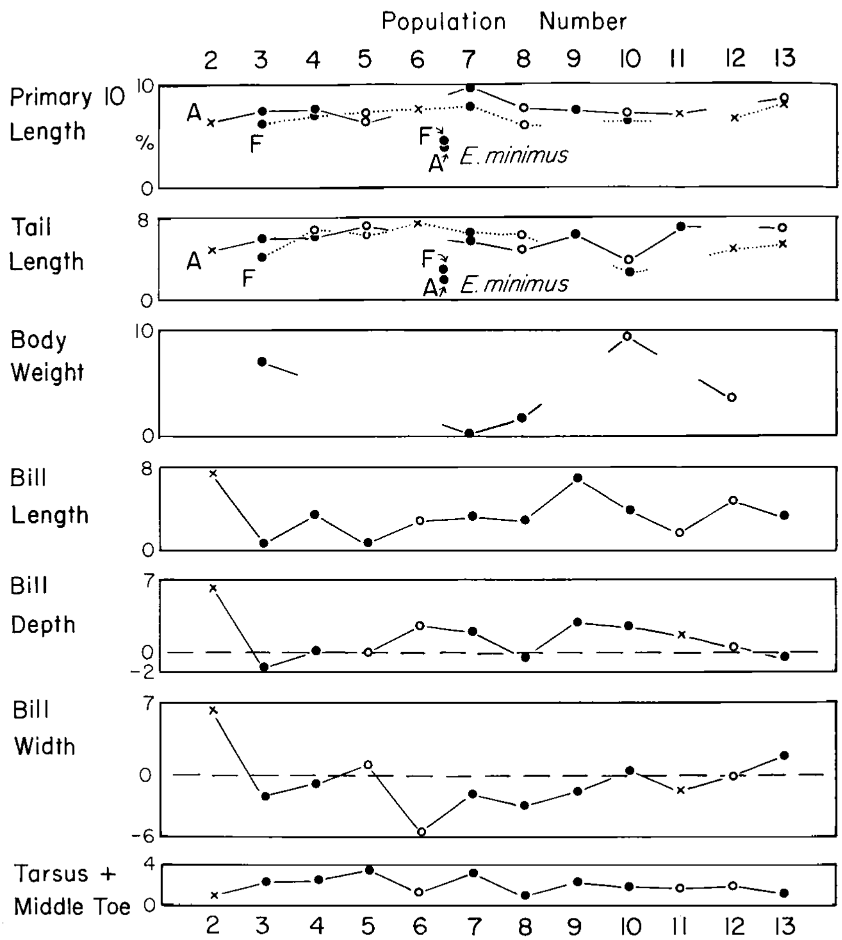

Figure 5. Sexual dimorphism in size in the Hammond's Flycatcher. An "X" represents a sample of fewer than 10 specimens each for both sexes; an open circle denotes a sample for which one sex was represented by fewer than 10 specimens. Gaps in record for upper three categories are for samples too small for meaningful treatment. For the length of the tenth primary and for tail length, adults (A) are separated from first-year birds (F), and values of percentage dimorphism in *Empidonax minimus*, calculated from data in Johnson (1963: 107), are included for comparative purposes in these two categories. The sample from population 1 is too small for analysis.

could well be during the breeding season when the members of a pair are confined to the territory where they must share the available food resources. See Rand (1952) and Selander and Giller (1963) for detailed discussion of sexual dimorphism in bill size and shape in other bird groups.

TABLE 6
MAXIMUM DIVERGENCE BETWEEN POPULATIONS

Character	Males		Females	
	Per cent divergence[1]	*Most divergent populations*	*Per cent divergence*[1]	*Most divergent populations*
Length of tenth primary				
Adults	3.2	8<13	1.8	7<9
First-year	2.6	3<10	1.7	7<10
Tail length				
Adults	3.4	6<12	2.1	4<9
First-year	2.8	3<9	3.5	7<10
Bill length	4.8	3<4	5.4	4<9
Bill depth	3.7	5<12	3.4	3<10
Bill width	4.8	3<13	4.0	3<8
Tarsus length plus middle toe length	2.8	5<8	2.0	7<10
Body weight	5.3	3<8	—	—

[1] Calculated by dividing the difference between the means of a character for the two most divergent populations, each of which is represented by 10 or more specimens, by the mean of that character for the entire species sample (see Tables 1–5).

DISCUSSION

The Hammond's Flycatcher shows a remarkable degree of interpopulational uniformity in several of the morphologic characters examined. For example, the two populations most divergent in length of the tenth primary differ by less than two per cent for females and slightly over three per cent for males (Table 6). Similar minor differences in percentage occur between the populations most divergent in length of tail and in length of tarsus plus length of middle toe. Low values of Coefficients of Variability, below 3.2 for entire species samples (Tables 1, 2, and 4), further attest to the limited variability of these characters.

Slightly greater interpopulational differences exist in bill dimensions and in body weight, where divergence percentages are between 3.4 and 5.4 (Table 6). High values of Coefficients of Variability for bill measurements, between 5.08 and 5.63 for entire species samples (Tables 3 and 4), and for body weight, between 4.72 and 9.10 (Table 5), also indicate that these characters are basically the most variable of those studied.

The minor geographic changes in size of this species seem to be rather chaotic or random in distribution, with little concordance among the several characters examined. There is clearly no evidence for size variation of a "subspecific degree" that might be expected in view of the suggestion of Jewett *et al.* (1953) that the Hammond's Flycatcher varies geographically in color, with two color types being segregated west and east of the Cascade Mountains. However, their suggestion needs to be investigated in detail when series of freshly molted birds are collected while still on their breeding grounds immediately before the fall migration.

The much larger recent samples verify fully the information on size presented earlier (Johnson, 1963) for this species. For length of the tenth primary, for example, means of the entire species samples reported in the present paper (Table 1) differ from the figures of 1963 by only .11 to .70 mm, depending upon the sex-age category. Similar ranges of difference between values given in this paper and those offered earlier are, for length of tail, .08 to .20 mm, and, for length of bill, from .03 to .04 mm. The latter two characters show striking conformity. Therefore it is reasonable to assume that the criteria of identification presented earlier that are based on primary feather ratios and on bill length, insofar as they are useful, appear to depend upon measurements which, although from small samples, adequately described the range of variation of these characters for the species.

Possible support for Salt's hypothesis.—In a recent discussion of geographic variation in body weight and in relative adaptation of populations of a number of species of birds in western North America, Salt (1963) proposed that the population of lightest weight of a species represents the "central," ancestral, and most highly adapted population of the species, that is, the population that gave rise to the more peripheral, heavier, and less adapted populations. The Hammond's Flycatcher, with an extensive breeding range that is essentially linear, with well defined "central" populations (5, 6, 9, and 10) and peripheral populations (1, 2, 8, and 13), would seem to be a species worth examining for a test of Salt's hypothesis. Unfortunately, only for populations 3, 7, and 8 are numbers of body weights sufficient for worthwhile analysis. For these populations it is notable that number 8 is both the lightest and one of the most peripheral, hence Salt's hypothesis is not supported unless we assume that this population in the Sierra Nevada is actually ancestral, and that the heavier, more northerly populations were derived from it. There is no good evidence at present to support such an assumption. Consideration of the low density of breeding birds leads to the belief that the Sierra Nevada is clearly marginal for *E. hammondii.* This species is much more common and occurs in more continuous habitat in the northwestern United States and southwestern Canada than in the "central" populations mentioned earlier. No trends in support of Salt's hypothesis are evident to me from examination of the few weights available from other sample areas, but more data are needed before additional comments on the presence or lack of correlation with Salt's view are justified.

Adaptive variation resulting from competition.—Intraspecific competition as a possible cause for divergence in bill shape between males and females has already been mentioned in the section on sexual dimorphism. Interspecific competition is less obviously demonstrable as influencing geographic change in morphology except for certain populations of British Columbia. In population number 4 of Vancouver Island the males average significantly longer in bill length than adjacent populations 3 and 5, to the northeast and east, respectively. On Vancouver Island, *E. hammondii* is abundant in the lowlands, essentially in the absence of the Western Flycatcher (*E. d. difficilis*), which breeds only rarely (Swarth, 1912: 43) or is uncommon locally in the lowlands. On the nearby coast of British Columbia and on the San Juan Islands, *E. d. difficilis* is abundant in coastal forest where *E. hammondii* is either rare or absent (Munro and Cowan, 1947: 150–151). Farther north on the Queen Charlotte Islands, *E. d. difficilis* is again abundant (Osgood, 1901: 46); *E. hammondii* is lacking. Distributional information concerning the Hammond's and Western flycatchers in the Great Basin and Rocky Mountains also points to competitive interaction of the two forms, the details of which will be presented more fully elsewhere (N. K. Johnson, MS) in connection with a systematic revision of *E. difficilis*.

The suggestion of a competitive relationship between these two species of *Empidonax* is reasonable also because their microhabitats, and probably their niches as well, are remarkably similar. Both the Hammond's Flycatcher and the Western Flycatcher forage in shade under the foliage canopy in canyon woodlands and dense forests on steep hillsides. They seem to be "ecologic equivalents" and competition between them is to be expected where they come into contact. I speculate that the population of the Hammond's Flycatcher on Vancouver Island has evolved longer-billed males in the absence of competitive pressure with the larger-billed Western Flycatcher. Presumably the longer bill of *E. hammondii* could serve in obtaining the larger insects which would perhaps ordinarily be more accessible to *E. difficilis*.

Females of population 4 also may have longer bills than those in adjacent populations, but the present samples do not show statistically significant differences. The lack of marked sexual dimorphism in bill length for the Vancouver Island population (Figure 5), however, implies that both sexes show the trend toward increased size. Possible adjustments in bill size or shape or both in the Western Flycatcher, which may result from competition with the Hammond's Flycatcher, remain to be investigated.

Population 3 of the Hammond's Flycatcher is partly in contact with the Least Flycatcher in central British Columbia at the western margin of the range of the latter species. Although detailed information on the nature of this contact of the two species is unavailable, it is appropriate to examine size characteristics of this population of *E. hammondii* to see if evidence exists for the occurrence of hybridization, ecologic interaction, or both, between the two species. Birds from population 3 have relatively tiny bills which are shorter and narrower than the bills of birds from adjacent population 9 as well as from those of populations 7 and 8 farther south. Conceivably this could be the result of an ecological interaction with *E. minimus*. Character displacement may exist between the two species in this area. One of the greatest consistent differences between the Hammond's and Least flycatchers is the shape of the bill, that of the latter species being both wider and deeper than that of the former. The narrower bills of birds from population 3 could exemplify character divergence that resulted from competition of the two species in sympatry, although this suggestion is purely speculative pending a refined study of the niche relations and ecologic interaction of the two forms in British Columbia.

It is significant that the Hammond's Flycatchers from population 3 are not smaller in other morphologic features, such as body weight. If such were true, it could support the notion that hybridization with the smaller Least Flycatcher occurs in the area. There is also no evidence for reduced sexual dimorphism (Figure 5) in population 3 which one might expect to find if interbreeding existed between *E. hammondii* and *E. minimus*; the latter species is less dimorphic.

The possible operation of "Allen's Rule" in the promotion of small bill size in northern populations of the Hammond's Flycatcher remains uncertain, and, in my opinion, is of dubious relevance to this species which is present in northern latitudes only during the summer breeding season.

Causes of morphologic stability.—Because of the structuring of a species into local populations or demes, and the presumed existence of selection for local adaptation to the different environments occupied by the various demes, geographic variation among populations of a species is to be expected. The apparent absence of such variation is usually attributable to insufficient study (Mayr, 1963: 302). However, certain species show great morphologic uniformity even after careful scrutiny, for example, the Brown-headed Nuthatch (*Sitta pusilla*) studied by Norris (1958) and the North American population of the European Tree Sparrow (*Passer montanus*) compared in the 1960's with the presumed descendants of the population in Germany from which it was derived in 1870 (J. C. Barlow, Abstracts of papers, 82nd Stated Meeting of Amer. Orn. Union, Lawrence, Kansas, p. 27, 1964; multilith.).

Possible explanations for the absence of geographic variation have been discussed lucidly by Mayr (1963: 302–304). For example, certain ducks are highly panmictic, evidently because of great dispersal and resultant intermixture of various populations of the species. This implies a lack of philopatry, which is defined by Mayr (1963: 670) as "The drive (tendency) of an individual to return to (or stay in) its home area (birthplace or other adopted locality)." This phenomenon, commonly known in birds as "Ortstreue" or "place faithfulness," varies widely in degree according to species, sex, and age (see discussion and examples cited by Welty, 1962: 225–227). To what extent the relative lack of geographic variation in the Hammond's Flycatcher results from reduction or absence of Ortstreue, which leads to panmixia, can be determined only after marking and recovery studies of breeding birds and of nestlings. Possibly also affecting the year to year composition of breeding populations of *E. hammondii* is the existence of sex and age differences in routes of the spring migration (Johnson, 1965). These differences conceivably could promote the eventual mating of birds from widely separated places of hatching.

Strong genetic homeostasis is also cited by Mayr as being responsible for morphologic uniformity. That the Hammond's Flycatcher shows great phenotypic stability is evident from the present study. Significantly, most species in the genus *Empidonax*, excluding perhaps the Buff-breasted Flycatcher (*E. fulvifrons*) and the Black-capped Flycatcher (*E. atriceps*), and one or two other species, seem to have what is basically the same general phenotype, if one disregards minor differences in color and size. Therefore, throughout the genus apparently "little of the genetic variation penetrates into the phenotype in the presence of strong homeostatic devices" (Mayr, 1963: 304). The fact that all species in the genus are sexually monomorphic in coloration of plumage provides another point of evidence for limited genetic penetrance into the phenotype. For a thorough discussion of the theory of genetic homeostasis, which provides for the retention of extensive genetic variability masked beneath a stable or standardized phenotype, see Lerner (1954) and Ehrlich and Holm (1963).

Limited ecologic tolerance may be operating in conjunction with or in addition to genetic homeostasis to preserve the uniformity of the phenotype in the Hammond's Flycatcher. The theoretical correlation between degree of ecologic tolerance and amount of racial diversity has been analyzed by Miller (1956) as part of his proposed "moderation thesis," which states that "Moderate innate ecologic tolerances of species rather than either sharp restriction or eurotopy [broad ecologic tolerance] seem to favor rapid polytypic diversification." The monotypic Hammond's Flycatcher supports this thesis by being rather narrow in nesting habitat requirements; it usually breeds in subalpine forest of spruce or fir, with lesser populations occurring in cool, mature lower montane forest and in northern aspen woodland. Indeed, specificity of breeding habitat seems to be the general rule for most species of *Empidonax*, an observation in accord with the low degree of polytypy. Several of the races currently recognized (Miller *et al.*, 1957) in certain species, for example in the

Mexican populations of the Western Flycatcher, are weakly founded and are probably unrecognizable (N. K. Johnson, MS). Other "well marked" forms currently treated as races, for example in the Traill's Flycatcher (*Empidonax traillii*), are probably full species (Stein, 1963). Most species of the genus *Empidonax*, including the Hammond's Flycatcher, apparently provide evidence in support of Miller's moderation thesis in that they each show rather restricted habitat occurrence and relatively limited geographic variation.

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SUMMARY

This paper discusses and describes geographic variation in size in the Hammond's Flycatcher (*Empidonax hammondii*), a species that nests in boreal forests from Alaska to New Mexico. The analysis is based on 545 specimens of summer residents which were divided for treatment into 13 geographic populations, were segregated by sex and age (first-year and adult categories), and were measured for the length of the tenth primary, tail length, bill length, bill depth, bill width, tarsus length, middle toe length, and body weight.

This species is remarkably uniform in size throughout its range; no pattern of variation exists which merits subspecific treatment. In certain sex-age categories minor significant differences for certain characters occur between populations. For the most part these differences seem to be random in distribution. In British Columbia, however, there is evidence that certain populations of the Hammond's Flycatcher have diverged in bill size, apparently in relation to the presence or absence of congeneric

species. For example, birds from the population on Vancouver Island, in the absence or rarity of the Western Flycatcher (*Empidonax difficilis*), a large-billed species with a similar ecologic niche, are significantly longer-billed than those from the adjacent mainland where Western Flycatchers are abundant. Birds from the population of the Hammond's Flycatcher in south-central British Columbia, some of which are sympatric with individuals of the closely related Least Flycatcher (*Empidonax minimus*), have significantly narrower bills than adjacent populations of the species. This may be an instance of character displacement and needs further detailed study. There is no morphologic evidence in *E. hammondii* from the area of sympatry that suggests the occurrence of interbreeding with *E. minimus*.

Intrapopulational comparisons of degrees of sexual dimorphism in several measurements of the bill strongly indicate divergence in bill shape between the sexes, with the females usually having shorter but wider bills than the males. Such differences may function to reduce intersexual competition for food between the members of a pair on their territory.

Reduction or absence of geographic variation, while possibly resulting from lack of Ortstreue, seems best attributed to strong genetic homeostasis for the standardized "*Empidonax* phenotype," homeostasis which masks the extensive genetic variability present. Sexual monomorphism in plumage may be an additional point of evidence for the presence of strong homeostatic forces. Limited ecologic tolerance in the Hammond's Flycatcher, a feature shared by many other species of the same genus, is also probably related to the existence of relatively slight geographic variation.

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