DIFFERENTIAL TIMING AND ROUTES OF THE SPRING MIGRATION IN THE HAMMOND FLYCATCHER

By Ned K. Johnson

Because banding returns and sight records of flycatchers in the genus *Empidonax* cannot be allocated safely to species, specimens of presumed migrants provide the only satisfactory information on timing and routes of migration. The Hammond Flycatcher (*Empidonax hammondii*) occurs widely as a migrant in western North America and numerous specimens of probable migrants have been preserved in collections. Incidental to work on the systematics and molts of several species in the genus *Empidonax* (Johnson, 1963*a*, 1963*b*) I gathered information on locality, date, sex, and age for 583 specimens of spring migrant *E. hammondii*; an analysis of these data is presented here. A basic assumption of this analysis is that the specimens of this monomorphic species were taken at random, so that the sex-age composition of museum samples is an accurate representation of the actual composition of the wild population in the particular area at the time of sampling. I am unaware of possible differences in behavior of migrant males versus females, or of first-year individuals versus adults, which could lead to bias in sampling, although I would not deny that certain differences might exist. Variation between seasons in timing and extent of collecting activities should be compensated for to some degree by the fact that the specimens upon which this report is based were taken in 86 different years, between 1865 and 1962.

The present compilation is based on dates and general localities for specimens of migrants, identified and aged according to criteria presented earlier (Johnson, 1963*a*). Hopefully, it will serve as groundwork for the analysis of future specimens of spring migrants of this species.

ACKNOWLEDGMENTS

In addition to the specimens in the Museum of Vertebrate Zoology, study material was examined from the following sources: American Museum of Natural History (through Wesley E. Lanyon), California Academy of Sciences (through Robert T. Orr), Carnegie Museum (through Mary A. Heimerdinger), Chicago Natural History Museum (through Emmet R. Blake), Denver Museum of Natural History (through Alfred M. Bailey), Los Angeles County Museum (through Kenneth E. Stager), Philadelphia Academy of Natural Sciences (through James Bond), San Diego Society of Natural History Museum (through Richard C. Banks), United States National Museum (through Philip S. Humphrey), British Columbia Provincial Museum (through C. J. Guiget), National Museum of Canada (through W. Earl Godfrey), Royal Ontario Museum (through James L. Baillie), University of Alberta (through Victor Lewin), University of British Columbia (through Ian McT. Cowan), University of Arizona (through Joe T. Marshall, Jr.), Colorado College (through Dorothy Mierow), University of Colorado (through Hugo G. Rodeck), Cornell University (through Charles G. Sibley), Dickey Collections at the University of California, Los Angeles (through Thomas R. Howell), University of Kansas Museum of Natural History (through Richard F. Johnston), Long Beach State College (through Dennis G. Rainey), Louisiana State University Museum of Zoology (through George H. Lowery, Jr.), Museum of Comparative Zoology at Harvard College (through Raymond A. Paynter, Jr.), University of Michigan Museum of Zoology (through

Robert W. Storer), Minnesota Museum of Natural History (through Dwain W. Warner), Montana State College (through Clifford V. Davis), Moore Laboratory of Zoology at Occidental College (through John W. McMenamin and John William Hardy), University of Nevada Museum of Biology (through Fred A. Ryser, Jr.), New Mexico State University (through Ralph J. Raitt, Jr.), University of Oregon (through J. A. Shotwell), University of Utah Museum of Zoology (through William H. Behle), University of Washington (through Frank Richardson), and Washington State University (through George E. Hudson). Specimens also were examined from the private collections of Gale Monson and Eugene A. Cardiff. I wish to thank the curators of these collections for their kind assistance and patience in loaning me specimens for this study and for other problems now under investigation in the genus *Empidonax*.

Carl Bock, George T. Ferrell, and Mercedes S. Foster helped handle data and provided stimulating discussion of the problem. William J. Hamilton III, William Z. Lidicker, Jr., William Salt, and Charles S. Thaeler offered constructive comments. The final versions of the illustrations were prepared by Gene M. Christman.

METHODS

A specimen was considered to represent a spring migrant if it had been collected between March 1 and mid-June at any locality removed from the known wintering range and the known breeding range of the species. Birds taken prior to May 20, at or near breeding localities, were also grouped with the migrants if they had inactive gonads and/or fat deposits. This procedure may have resulted in the inadvertent inclusion of a few recently arrived summer residents in the samples from northern areas, such as Washington and British Columbia, where the period of spring migration is attenuated and imperceptibly merged with the breeding season.

Because individuals of species which are monomorphic in plumage can be missexed easily during the season of migration when gonads are undeveloped, wing length, wing formula information, tail length, and bill dimensions were recorded for each specimen as verification or refutation of the sex designation on the specimen tag. Specimens believed to be mis-sexed were included with the opposite sex for analysis if the value for the length of primary 10 fell outside of the range of values expected for the particular sex-age category on the basis of measurements obtained from breeding birds from all parts of the summer range of the species (Johnson, *in press*). For 246 breeding adult males, 57.2 mm. was the lowest value recorded for the length of primary 10; for 129 breeding first-year males, 55.4 mm. was the lowest value recorded. Therefore, a specimen of a migrant bird marked "♂" with a value lower than ever recorded for a breeding bird of a comparable age category was considered to be a female. For 106 breeding adult females, 60.4 mm. was the highest value recorded for the length of primary 10; for 64 breeding first-year females, 59.8 mm. was the highest value recorded. Therefore, a migrant bird marked "♀," yet with a higher value for the length of primary 10 than ever recorded from a breeding individual of a comparable age category, was considered to be a male in the calculations. This conservative procedure required the changing of sex for less than three per cent of the specimens analyzed. Breeding birds were used as standards for comparison because of the high probability that they were correctly sexed.

To enable statistical treatment of timing of migration, the date for each specimen was converted to a number on a scale of 100, beginning with March 1 as number 1 and ending with June 10 as number 100. Each month is valued at 30 units; hence, April 15 equals "45," May 4 equals "64," and so on. For March and May, each of which have 31 days, birds taken on the last day of the month were grouped with those from the thirtieth of the month. See figures 2 and 3 to equate particular "migration date values" with actual spring dates.

ROUTES OF THE SPRING MIGRATION

The localities of all specimens examined of presumed spring transients through northern México and western North America are plotted in figure 1. Sixteen sample areas include most, but not all, of the specimens; it is between these areas that comparisons are made. I attempted to keep the sample areas small so as not to obscure possible differences in timing between adjacent areas, yet large enough to encompass meaningful numbers of specimens. Because the Hammond Flycatcher winters as far south as Honduras, considerable migration certainly takes place south of northern México, where I began the organization of sample areas. Such movement through or near wintering areas was not analyzed in detail because aggregate numbers of specimens are small and because it is difficult to discriminate between spring migrants and late winter residents collected in such regions.

To a considerable degree the concentrations of specimen localities represent nothing more than regional differences in collecting effort. This is particularly true of southeastern Arizona (sample area 2) and the deserts and coastal lowlands of southern California (sample areas 4 and 5), where extensive collecting over many seasons has resulted in large samples (a total of 363 specimens from these three sample areas have been examined). However, birds have been collected intensively in other regions in the western United States without the taking of equivalent numbers of Hammond Flycatchers. For example, only eight specimens of this species have been examined from the San Francisco Bay area (sample area 8). Sample sizes may therefore give some indication of regional differences in abundance which suggest differences in routes of migration. The relative differences in sample size between areas 5 and 8 probably reflect actual differences in intensity of migration. Possibly most of the birds from sample area 5 move inland and follow the axes of the Tehachapi Mountains and the Sierra Nevada, where collecting has been relatively slight in the early spring, leaving comparably fewer birds to pass through the Central Valley and along the Central Californian coast.

The bulk of the spring migration of the Hammond Flycatcher passes through the far West (fig. 1). This correlates well with the breeding distribution of this species, which is centered in the northwestern part of the United States and in southwestern Canada (Johnson, 1963*a*, map p. 142). This species is less numerous in other parts of the breeding range; populations in the Rocky Mountains of New Mexico, Utah, and Colorado, those in two isolated ranges in eastern Nevada, and those breeding in the Sierra Nevada of California are considered marginal.

Because the samples from areas 2, 4, and 5 are large, much of the meaningful discussion in this paper will relate to those samples. Sample 2 from southeastern Arizona and northeastern Sonora is considered to represent most accurately the actual composition of the migratory population in the spring because (1) this is the largest of any migrant sample studied (160 specimens); (2) this sample spans the longest period of the spring migration of any sample considered (76 days); (3) this sample is from an area geographically located so as to intercept the probable center of the migratory front entering the United States from México; and (4) the composition of this sample does not deviate significantly (Chi-square = 4.07, for three degrees of freedom, where values above 7.81 are significant at the 95 per cent level) from that

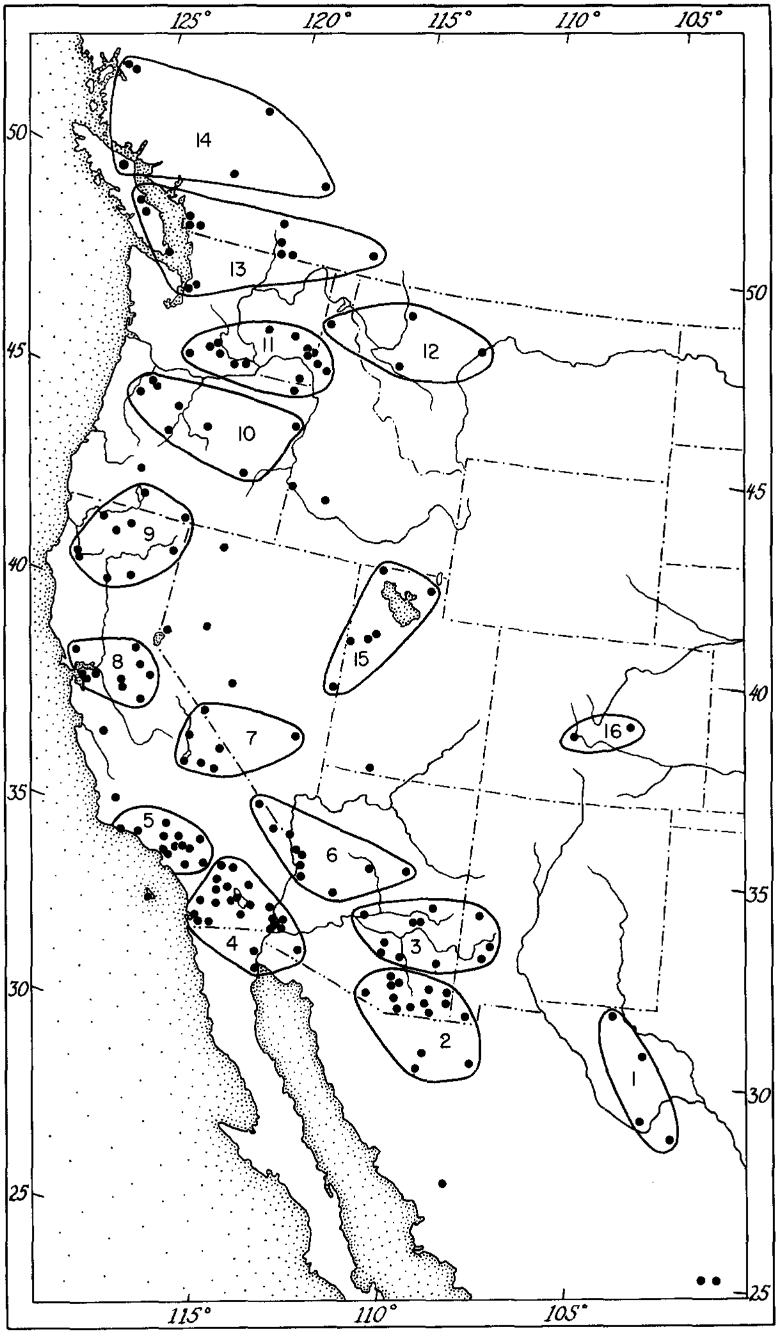

Fig. 1. Map showing the distribution of spring migrant *Empidonax hammondii* in western North America. Dots refer to localities represented by museum specimens. The 16 areas, each outlined by a solid line, include the localities represented by samples used for comparison.

TABLE 1

COMPOSITION OF SAMPLES OF SPRING MIGRANT HAMMOND FLYCATCHERS

Sample	Ad. ♂♂		1st yr. ♂♂		Ad. ♀♀		1st yr. ♀♀		Total
area no.	No.	Per cent	No.	Per cent	No.	Per cent	No.	Per cent	No.
1	3	20.0	7	46.7	2	13.3	3	20.0	15
2	68	42.5	35	21.9	29	18.1	28	17.5	160
3	12	60.0	4	20.0	2	10.0	2	10.0	20
4	36	41.4	27	31.0	17	19.5	7	8.1	87
5	69	59.5	21	18.1	23	19.8	3	2.6	116
6	8	30.8	4	15.4	11	42.3	3	11.5	26
7	1	8.4	4	33.3	3	25.0	4	33.3	12
8	5	45.4	3	27.3	3	27.3	—	—	11
9	12	57.1	5	23.8	4	19.1	—	—	21
10	6	60.0	3	30.0	1	10.0	—	—	10
11	21	63.6	7	21.2	5	15.2	—	—	33
12	12	85.8	1	7.1	1	7.1	—	—	14
13	23	74.2	5	16.1	2	6.5	1	3.2	31
14	6	60.0	2	20.0	2	20.0	—	—	10
15	5	38.5	3	23.1	1	7.7	4	30.7	13
16	3	75.0	—	—	1	25.0	—	—	4
									583

of a sample of 200 specimens from the wintering range (November 1 through February 28), whose proportions are: adult males, 47.0 per cent; first-year males, 17.5 per cent; adult females, 20.5 per cent; and first-year females, 15.0 per cent (Johnson, MS). The proportions of the different sex-age categories in sample 2 are as follows: adult males, 42.5 per cent; first-year males, 21.9 per cent; adult females, 18.1 per cent; and first-year females, 17.5 per cent. Marked deviations in proportions of the sex-age groups in other migrant samples are believed to reflect actual differences in use of migratory routes by birds assigned to the various categories, after the birds pass through southeastern Arizona.

Table 1 lists the sizes and proportions of the sex-age groups for all samples. In table 2 is presented an analysis of significance of differences between the sample areas in their proportions of the various categories. Two trends, apparent from an examination of these tables, provide evidence that the adult males and the first-year females do not migrate north in the spring with a uniform geographic distribution in the western United States. Although the adult male category of area 4 is not significantly different from that of area 2, there is a significant increase in adult males, starting with area 5 in southern California, northward through the Pacific states from sample areas 8 through 14. This relative abundance of adult males in the coastal samples is apparently compensated for by a shortage of this category in certain of the interior samples (areas 6 and 7). The reverse of this situation is seen in the first-year females which seem to favor the interior route on their way north. Along the coast there are significantly fewer first-year females in areas 4 and 5, and none from samples 8 through 14, except for one specimen from area 13. This relative scarcity and/or absence of first-year females in the samples from the Pacific seaboard is offset apparently by their relative abundance in at least two interior samples (areas 7 and 15). I feel that this evidence is strong enough to support the notion of differential pathways of migration for the adult males and for the first-year females.

TABLE 2

EVIDENCE FOR DIFFERENTIAL ROUTES OF MIGRATION AMONG SEX-AGE CATEGORIES OF THE HAMMOND FLYCATCHER

Sample area[1]	Chi-square[2]	Deviant categories[3]
3	2.82	—
4	7.82*	First-year males (+) First-year females (–)
5	23.57**	Adult males (+) First-year females (–)
6	10.32*	Adult males (–) Adult females (+)
7	6.06	Adult males (–) First-year females (+)
(8 + 9 + 10)	9.29*	Adult males (+) First-year females (0)
11	9.47*	Adult males (+) First-year females (0)
12	10.82*	Adult males (+) First-year females (0)
13	13.65**	Adult males (+) First-year females (–)[4]
14	1.47	Adult males (+) First-year females (0)
15	2.15	First-year females (+)

[1] Areas 1 and 16 have too few specimens for analysis; area 2 is the standard used for comparison.
[2] Obtained by using the data from area 2 as the basis for the determination of theoretical frequencies. For three degrees of freedom, Chi-square values above 7.81 are significant at the 95 per cent level ($p = 0.05$; these are marked with one asterisk), and values above 12.84 are significant at the 99.5 per cent level ($p = 0.005$; two asterisks).
[3] Categories noted during the computation of Chi-squares to be most deviant from the theoretical frequencies. A plus sign follows categories for which the observed frequency was significantly higher than the theoretical frequency, a minus sign is used for categories for which the observed frequency was significantly lower than the theoretical frequency. Zeros following certain first-year female categories indicate the absence of specimens. Certain samples (for areas 3, 7, 14, and 15) are too small to show significant differences by the Chi-square method; for these the deviant categories indicate probable trends only.
[4] One specimen of a first-year female.

I am unable to account either for the significantly greater numbers of first-year males in area 4 or for the relative abundance of adult females in area 6, because no trends are apparent when regions are compared. No shortages of comparable categories exist in adjacent sample areas which might compensate for the apparently greater numbers of those particular groups in areas 4 and 6. Other than these two exceptions, the first-year males and the adult females seem to maintain expected proportions in all other samples compared with area 2.

TIMING OF THE SPRING MIGRATION

Data on timing of migration have been analyzed in several ways. The average time of arrival in a particular sample area is shown in figures 2 and 3, by the use of a lower case "a" on samples of ten or more specimens. This letter denotes the mean date of the six earliest specimens for that area. This method of calculation of

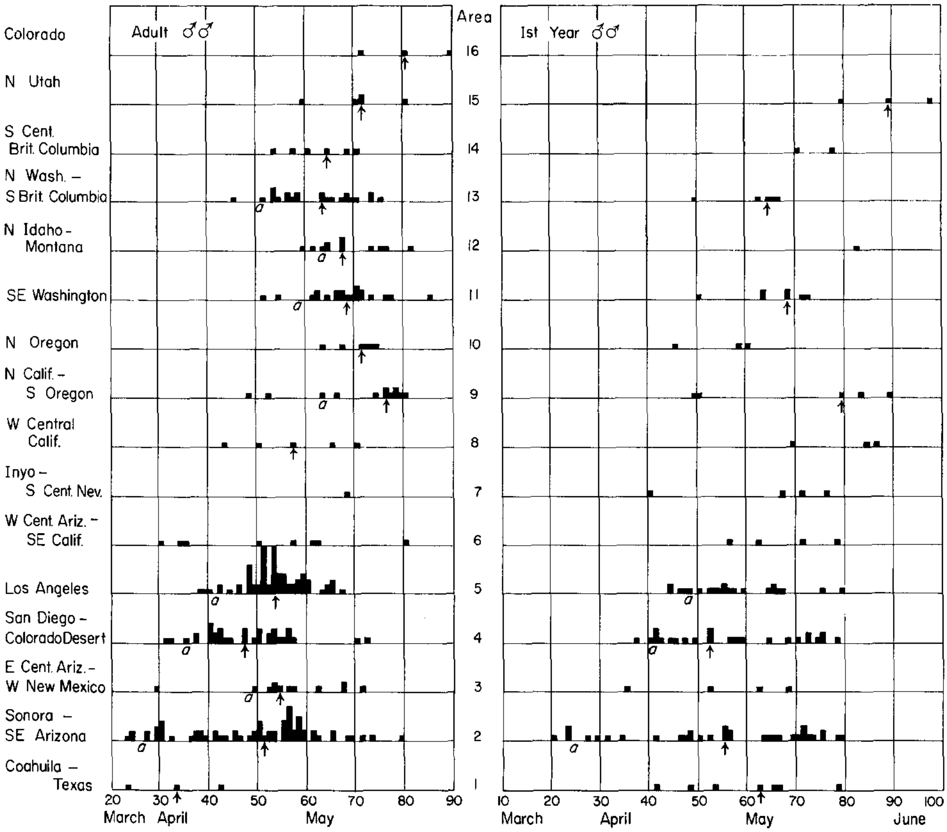

Fig. 2. Distribution by date of male specimens of *Empidonax hammondii* organized into sample areas. The letter "a" denotes the average time of arrival based on the mean date of the six earliest records for samples of 10 or more specimens. The small vertical arrows refer to median dates of spring passage.

the average time of arrival probably moderates the effects of extreme seasonal variation. The actual date of arrival of the Hammond Flycatcher in a region is certainly earlier than that indicated, because of this method of calculation, and because the species was not necessarily collected immediately upon its arrival.

In figures 2 and 3 all specimens are plotted by date for each sample area. Figure 4 and table 3 summarize these data on timing and present statistics to support statements on significance of differences in scheduling of migration through areas represented by samples large enough for comparison. Because each method of measuring central tendency has its special merits, medians (arrows in figures 2 and 3), means (table 3), and modes (table 4) have been calculated.

Timing differences between sample areas.—For area 1, in northern Coahuila and western Texas, limited data show the relatively early presence of adult males (figs. 2 and 4). Unless spring passage is protracted, some of these birds may be destined to migrate westward through Arizona, rather than northward across New Mexico to Colorado, because arrival dates for the latter area are comparatively late

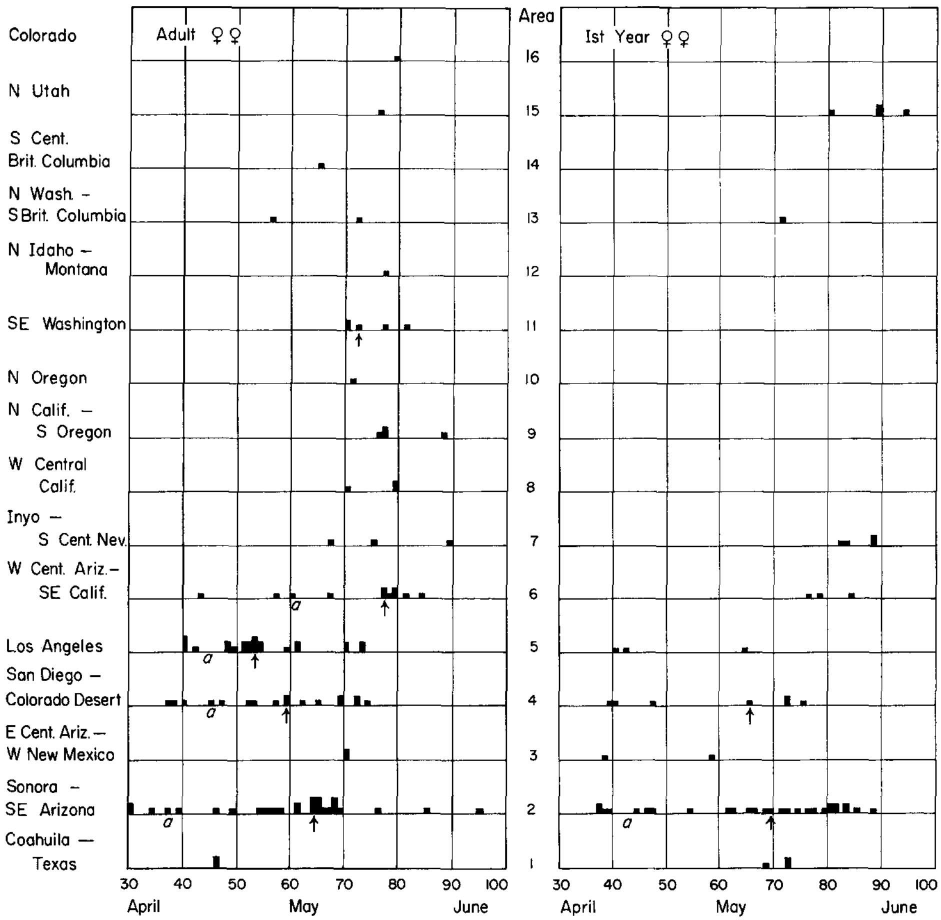

Fig. 3. Distribution by date of female specimens of *Empidonax hammondii* organized into sample areas. See legend of figure 2 for further explanation.

(mid-May), indicating that the late March and early April Texan and Coahuilan birds are not involved. Interestingly, the seven first-year males were collected later than the adults and showed only slight overlap with the older birds. The three first-year females from area 1 similarly were collected approximately three weeks later than the two adult females.

In area 2 there is an indication of bimodal distribution within each sex-age category, particularly in the adult males. For this reason the data have been handled for both unimodal and bimodal distributions in tables 3 and 4 and in figure 4. The first mode (2A) in late March and early April may relate to the early passage of birds destined to migrate through areas 4 and 5, along the coast of southern California. The second mode (2B) in late April may involve birds destined to pass through areas 3, 6, and 7, in the interior of the southwest. Gradual northward progress from California to British Columbia between areas 8 and 11 may be seen in figures 2 and 3.

The early arrival of birds in areas 13 and 14 is notable for a region so far north;

TABLE 3

SPRING MIGRATION DATE VALUES[1] FOR THE HAMMOND FLYCATCHER

Sample area[2]	Sex	Age group	Number of specimens	Range	Mean with standard error	Standard deviation
1	Male	Ad.	3	24–43	33.00[3]	—
		1st yr.	7	42–79	60.15	—
	Female	Ad.	2	47	—	—
		1st yr.	3	69–73	71.35	—
2	Male	Ad.	68	24–80	49.70 ± 1.63	13.45
		1st yr.	35	21–80	55.00 ± 3.11	18.40
	Female	Ad.	29	31–96	61.45 ± 2.68	14.45
		1st yr.	28	38–89	66.75 ± 3.16	16.70
2A	Male	Ad.	23	24–46	33.85 ± 1.46	7.00
		1st yr.	10	21–47	30.50 ± 2.82	8.95
	Female	Ad.	7	31–50	38.70	—
		1st yr.	8	38–55	43.00	—
2B	Male	Ad.	45	46–80	57.78 ± 1.08	7.25
		1st yr.	25	48–80	64.80 ± 2.04	10.20
	Female	Ad.	22	55–96	67.30 ± 2.10	9.85
		1st yr.	20	62–89	76.75 ± 1.66	7.45
3	Male	Ad.	12	30–72	56.30 ± 3.40	11.80
		1st yr.	4	36–69	55.50	—
4	Male	Ad.	36	32–73	48.85 ± 1.54	9.25
		1st yr.	27	38–79	57.25 ± 2.59	13.20
	Female	Ad.	17	38–75	57.70 ± 2.91	12.00
		1st yr.	7	40–76	60.15	—
5	Male	Ad.	69	39–68	54.10 ± 0.78	6.50
		1st yr.	21	45–80	58.25 ± 2.22	10.20
	Female	Ad.	23	41–74	55.15 ± 2.08	10.00
		1st yr.	3	41–65	49.70	—
6	Female	Ad.	11	44–85	71.65 ± 3.76	12.50
		1st yr.	3	77–85	79.65	—
7	Female	Ad.	3	68–90	76.35	—
		1st yr.	4	83–89	85.50	—
9	Male	Ad.	12	49–81	71.33 ± 3.23	11.20
		1st yr.	5	50–90	70.00	—
11	Male	Ad.	21	52–86	68.95 ± 1.74	8.00
		1st yr.	7	51–73	65.85	—
12	Male	Ad.	12	60–82	68.85 ± 2.20	7.65
		1st yr.	1	83	—	—
13	Male	Ad.	23	46–76	62.15 ± 1.72	8.25
		1st yr.	5	50–67	62.00	—

[1] See page 424 for an explanation of the derivation of these values.
[2] Data not presented where information is fragmentary.
[3] Standard errors and standard deviations not calculated for samples of less than 10 specimens.

the evidence, at least from museum specimens, suggests that the Hammond Flycatcher appears in northern Washington, southern British Columbia, and Vancouver Island before arriving in certain more southerly interior areas such as northern Utah, Colorado, northern Idaho, and Montana (sample areas 15, 16, and 12). It remains

TABLE 4

MODES OF MIGRATION IN THE HAMMOND FLYCATCHER

Sample area number	Ad. ♂♂	1st yr. ♂♂	Ad. ♀♀	1st yr. ♀♀
	(Most specimens per 5-day interval)			
2A	28–32	24–28	31–35	38–42
2B	56–60	70–74	65–69	80–84
3	53–57[1]	—[2]	—	—
4	41–45	42–46	—	—
5	52–56	53–57	52–56	—
9	77–81	—	—	—
11	68–72	—	—	—
12	64–68	—	—	—
13	54–58	—	—	—
	(Most specimens per 10-day interval)			
2A	30–39	—	31–40	38–47
2B	51–60	56–65	61–70	77–86
3	50–59	—	—	—
4	41–50	43–52	—	—
5	49–58	51–60	46–55	—
11	63–72	—	71–80	—
12	60–69	—	—	—
13	57–66	—	—	—

[1] Samples of less than 15 specimens are underlined.
[2] Gaps indicate samples too small for meaningful analysis.

to be determined through banding studies whether these apparently later arriving interior birds represent (1) individuals that passed early through the southwest then northward through the Pacific states prior to heading northeast and/or east, or, (2) birds that merely migrated later directly northward through the Great Basin and Rocky Mountains region.

The span of records indicates to some extent the intensity of collecting in particular areas. Certain trends are apparent, however, one of which is the more rapid passage of birds along the coast (4 to 5 weeks) and the more leisurely migration through the interior (7 to 8 weeks). This difference is at least suggested by all sex-age groups, even where the samples are fairly small.

Differential timing of the spring migration by sex-age groups.—Intra-area differences in scheduling of the spring migration are evident between some of the sex-age groups although the pattern is complex and different from one region to another. In timing of mode A of area 2, the adult males may be earlier than either age group of females, but the samples of the latter sex are too small to establish this supposition. The adult males are not significantly different from the first-year males in timing of mode A. In scheduling of mode B of sample area 2, however, adult males are signif-

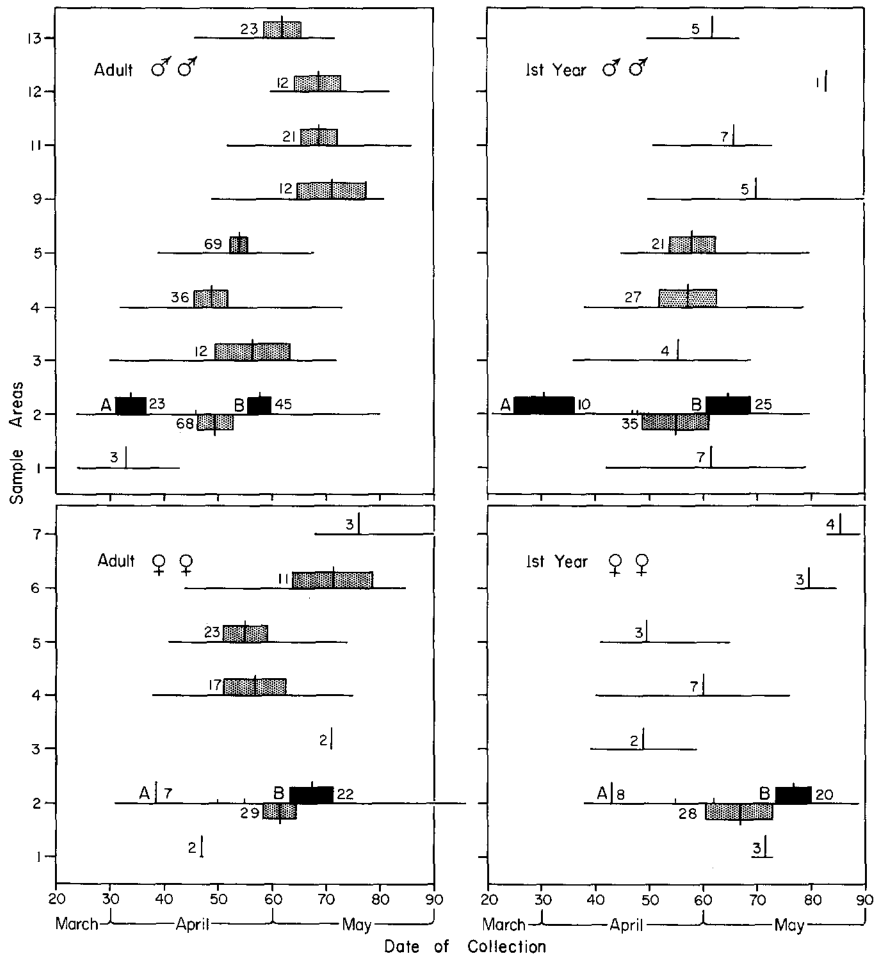

Fig. 4. Statistical analysis of specimen dates of spring migrant *Empidonax hammondii* from certain sample areas. Horizontal line of each figure represents the sample range. Vertical line of each figure represents sample mean. Rectangle on each side of mean delineates a distance equal to value of twice standard error of mean. Black rectangles for samples from area 2 are based on statistics that assume a bimodal distribution of dates for these samples.

icantly earlier than all other sex-age groups. Although the adult females and first-year males seem to be the same in timing of mode B, the first-year females are significantly later than either of those groups.

If the sample from area 2 is considered to have a unimodal distribution, then the adult males are scheduled significantly earlier than either age group of females, but not earlier than the first-year males. The latter group migrates significantly earlier than the first-year females, but not earlier than the adult females.

In area 4 the adult males are timed significantly earlier than the first-year males. The latter group is scheduled at about the same time as the adult females. Although there is slight overlap between twice the standard errors of the means, when adult females are compared with adult males, I believe that a larger sample would establish a significant difference between these two groups. First-year females are almost certainly timed later than at least the two age groups of males, but apparently too few of the former category pass near the coast to enable proper comparison.

In area 5 the adult males, first-year males, and adult females all appear to reach a peak at about the same time, although the bulk of the first-year males and the adult females seem to arrive later and leave later than the adult males. The three first-year females from area 5 do not seem to deviate in their timing from the other three sex-age groups.

In area 11 the adult males are almost certainly timed ahead of the adult females (table 4), although the small sample size for the latter group does not enable a positive statement. Within other sample areas, possible intra-area differences in timing between the various sex-age categories have not been detected, probably because of the small numbers of specimens at hand.

In general, the data show that in any given sample area the bulk of the first migrants to appear are adult males, followed by an influx of first-year males and adult females. The last migrants passing through an area are typically first-year birds, often females. The situation from one area to another is complex, however, and exceptions to these generalizations are to be expected when larger samples are available.

DISCUSSION

Ornithologists have long been interested in the subject of sex and age differences in timing and routes of migration. Most information appears to be available for the fall migratory period, when adults of certain species can be distinguished from birds-of-the-year on the basis of degree of skull ossification and/or distinctive plumage. Tordoff and Mengel (1956) provide a historical summary of the subject and offer useful discussion of differential fall migration of sex and age classes in several species. An example of a recent study of this topic is the paper by Schifferli (1963), who demonstrated sex and age differences in the timing and duration of fall migration of Chaffinches (*Fringilla coelebs*) through Switzerland.

Different patterns of spring migration by age categories seem to be less well understood, perhaps because in many species of passerine birds age groups cannot be discriminated at that season. Nolan and Mumford (1965:328), however, were able to establish that in the Prairie Warbler (*Dendroica discolor discolor*) the old males have an earlier spring migration than the old females, and also "probably earlier than does either sex among the yearling birds," based upon 162 birds killed at a television tower in the period from March 15 through May 13. They found that the average date of death for the adult males was April 9, whereas that for the other three sex-age classes was April 19. These authors further presented facts concerning first-year female Prairie Warblers that seem to parallel those for the Hammond Flycatcher, namely, that there is an apparent scarcity of this group in the spring that may reflect their use of a different route or of a different temporal pattern of movement from the other categories.

That the sexes may differ in timing of migration seems to be commonly known. In a recent treatise on migration Dorst (1963:252) wrote: "In the spring, the two sexes may migrate together, but the males are usually the first to arrive in the north. They select the territory in the nesting area, defend it against invasion by other males, and act as hosts to the females when they arrive." Recent examples of males migrating earlier than females in the spring in several species of passerines have been mentioned by Brewer and Ellis (1958).

In the genus *Empidonax* it is generally accepted that the males are the first to arrive on the breeding grounds; however, this is usually based on the unsatisfactory circumstantial evidence of the apparent earlier presence of singing males. Even if the females did arrive on the breeding area at the same time as the males, they could easily escape detection or be passed off as migrant individuals because of their comparatively unobtrusive behavior. Data from several regions presented in this paper strongly suggest that the adult males in the spring do migrate ahead of the adult and first-year females, and hence adult males would be expected to arrive first on the breeding grounds.

Why the adults usually migrate ahead of the first-year birds of the same sex is less easily understood. The earlier passage of adults may relate to their overall greater physiological and behavioral vigor and/or to their more highly perfected orientation abilities resulting from longer experience. However, beyond these general speculations it seems unjustified to attempt explanation of this timing difference in the almost total absence of pertinent facts.

One of the unexpected results of the present study is the evidence for differential migratory routes for adult males versus first-year females. This finding, together with the fact of earlier migration by the adult males, provokes an attempt to find the possible adaptive significance in these differences. The early passage of adult males very likely is related to the selective advantages of their early arrival in breeding habitat for territorial establishment. Because the coastal route apparently favored by the adult males is somewhat devious, particularly that portion through sample areas 4 and 5 in southern California, one wonders if the use of this route is adaptive for those individuals "requiring" early passage. Perhaps the coastal route is climatically more favorable for early spring passage than is the interior route (through areas 6, 7, and 15, for example) because of better food production for these flycatchers that prey upon small aerial insects. If this is granted, with the gradual onset of more favorable climatic conditions and food supply in the interior, later migrants could progressively use that more direct route, rather than the more devious coastal route. This suggestion is purely speculative and needs to be tested through widespread sampling of aerial insects at many different sites of spring migration of the Hammond Flycatcher in the southwestern United States. In any event, the different timing of peaking of the spring migration period within a given sample area by the various sex-age classes may well be an evolved response that adaptively functions to spread temporally the impact of the species as a whole on the food resources.

Although this report is based on nearly 600 specimens of spring transients, the need for further concentrated collecting of migrant *Empidonax hammondii* in certain regions during the spring season is evident. Many of the sample areas delineated in this paper are too large and encompass too few specimens for satisfactory analysis. Reference to figures 1 to 3 should enable a collector to note the gaps in the record for his area of particular interest and to plan the timing of future trips accordingly.

The widespread banding program now in effect for species of *Empidonax* flycatchers should continue, but with one proviso. A banded *Empidonax* recovered alive, even at a short distance away from the banding site, should be killed and preserved in a museum collection. Likewise, remains of banded *Empidonax* found dead should be saved for study. This would permit positive species determination and also enable the subsequent verification of the identification. Sex and age of such museum specimens can be determined with good reliability through wing measurements, wing formulae, and plumage examination. By this means satisfactory information on the routes and timing of individuals could be obtained, granted that the probable low recovery rate would permit only a very slow accumulation of facts. Banding records and recoveries of *Empidonax* based upon the species identifications of banders are worthless unless subsequent affirmation of the identifications is possible through reference to museum specimens.

SUMMARY

The Hammond Flycatcher (*Empidonax hammondii*) breeds in western North America from Alaska to California and northern New Mexico and winters chiefly from northern México to Honduras. Spring migration through northern México and the western United States occurs from mid-March through early June. Museum specimens provide the only satisfactory information on timing and routes of migration because identifications of banding recoveries and sight records are unreliable. A total of 583 museum specimens of presumed spring migrants of known sex and age have been organized into geographic sample areas for comparative statistical analysis of population composition and timing of spring movement. Because the Hammond Flycatcher is monomorphic and the sexes are not known to exhibit behavioral differences while migrating, collecting was presumably random.

The proportions of the different sex-age categories in a sample of 160 specimens from southeastern Arizona and northeastern Sonora (adult males, 42.5 per cent; first-year males, 21.9 per cent; adult females, 18.1 per cent; and first-year females, 17.5 per cent) are considered to represent most accurately the actual composition of the migratory population in the spring. Marked deviations in proportions of the sex-age groups in other samples are believed to reflect actual differences in use of migratory routes by birds assigned to the various categories, after the birds pass through southeastern Arizona. Spring migrants passing through southern Arizona seem to occur in two waves. The first wave, composed of birds probably destined to migrate west-northwest or northwestward through the Pacific states, consists of proportionately more adult males and fewer first-year females than in the population at large. The second wave of birds, probably destined to move in general toward the north or the north-northwest through the interior, is composed of relatively fewer adult males and more first-year females. It is suggested that the early migrants may have evolved the coastal route in response to more favorable climatic conditions leading to better production of aerial insects there than in the Great Basin and northern Mojave Desert in the early spring.

Limited evidence suggests that coastal migration through a given sample area lasts from three to five weeks, whereas interior migration lasts from seven to eight weeks. Of the four sex-age groups passing through a given sample area, adult males typically arrive first, followed by the first-year males and the adult females. First-year females usually arrive last and reach a peak latest. Differential timing of peaking by sex-age groups in one sample area is probably adaptive in that it moderates the impact of the species as a whole on the available food resources.

It is recommended that banding of *Empidonax* should continue only if recaptured birds are killed and placed in museums where accurate identifications can be worked out through critical study of the specimens. Identifications made at the time of initial banding usually are worthless.

LITERATURE CITED

Brewer, R., and Ellis, J. A.

1958. An analysis of migrating birds killed at a television tower in east-central Illinois, September 1955–May 1957. Auk, 75: 400–414.

Dorst, J.

1963. The migrations of birds (Houghton Mifflin Co., Boston).

Johnson, N. K.

1963*a*. Biosystematics of sibling species of flycatchers in the *Empidonax hammondii-oberholseri-wrightii* complex. Univ. Calif. Publ. Zool., 66:79–238.

1963*b*. Comparative molt cycles in the tyrannid genus *Empidonax*. Proc. XIII Int. Ornith. Congr. (Ithaca), 1962, 2:870–883.

1965. Morphologic stability versus adaptive variation in the Hammond Flycatcher. Auk, 82:*in press*.

Nolan, V., Jr., and Mumford, R. E.

1965. An analysis of prairie warblers killed during nocturnal migration. Condor, 67:322–338.

Schifferli, A.

1963. Vom Zug der Buchfinken (♂♂ und ♀♀) *Fringilla coelebs* in der Schweiz. Proc. XIII Int. Ornith. Congr. (Ithaca), 1962, 1:468–474.

Tordoff, H. B., and Mengel, R. M.

1956. Studies of birds killed in nocturnal migration. Univ. Kansas Publ. Mus. Nat. Hist., 10:1–44.

Museum of Vertebrate Zoology, University of California, Berkeley, California, December 25, 1964.