SPRING MIGRATION OF THE WESTERN FLYCATCHER, WITH NOTES ON SEASONAL CHANGES IN SEX AND AGE RATIOS

By Ned K. Johnson

The phenomenon of differential timing and routes of migration by sex and age groups within a species continues to provide a fascinating yet confounding element in the interpretation of seasonal movements of birds. In a convincing demonstration of seasonal and geographic differences in sex and age ratios of the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*), King et al. (1965) remind us that documentation of such differential migration is adequate for surprisingly few species. The problem is particularly difficult for the spring period when, in the absence of workable criteria enabling distinction of age classes for most species, possible age differences in migratory behavior remain obscured.

Specimens of migrant *Empidonax* flycatchers are numerous in scientific collections and afford reliable bases for description of routes and of timing of seasonal movements of sex-age categories in species for which sight records are unsatisfactory. The lack of sexual dimorphism in these flycatchers (except for a minor size difference) means that within a species the specimens were taken at random and, therefore, without bias for sex and age, so that the records which they represent may be treated statistically. Two such analyses, of spring and of fall migration in the Hammond Flycatcher (*Empidonax hammondii*), have been presented earlier (Johnson, 1965, 1970). The Western Flycatcher (*Empidonax difficilis*) is a suitable subject for a similar study and the present paper deals with an analysis of differential scheduling and routes of the spring migration in sex and age categories of the coastal form (*E. d. difficilis*) of this species.

MATERIALS AND METHODS

A museum specimen was considered to be a spring migrant if it had been collected between 15 March and 30 June at a locality removed from known sites of wintering or breeding. For southern California, northern Baja California, and southern Arizona, 229 specimens of spring migrants were examined; the study concentrates on this region where samples are fairly large. An additional sample of 35 specimens from the region of South San Francisco Bay (Palo Alto sample area) was included for comparative purposes. Specimens from other areas are too scattered in time and space to permit meaningful analysis. A total of 671 specimens from other seasons were also used incidentally in this report to document comments on seasonal changes in sex and age ratios.

For statistical treatment of timing of migration the collection date of each specimen was converted into a "migration date value," starting on 16 March (= 1) and ending on 30 June (= 107). Under this system, for example, a specimen taken on 29 April would have a migration date value of 45 and a bird taken on 11 June, a value of 88. Routine statistics of dispersion were then calculated from these values for samples of specimens from relatively restricted areas. Specimens were aged as "first-year" or "adult" on the basis of criteria to be published elsewhere (Johnson, 1974). These criteria are similar to those published previously for other species of *Empidonax* (Johnson, 1963:90-117) and depend on an understanding of cycles of feather replacement. Knowledge of molt cycles permits the recognition of the distinctive shape, color, and texture of juvenal feathers retained in first-year birds.

Specimens of *Empidonax* taken during the non-breeding season, when gonads are undeveloped, are often mis-sexed. Therefore, I measured each specimen to permit assessment of the sex designation noted by the collector on the label and to attempt to determine sex when such data were lacking. Measurements of large samples of breeding birds (Table 1) were used as standards of comparison because of the high probability that these birds were correctly sexed

TABLE 1. Measurements of breeding samples of *Empidonax difficilis difficilis*.[a]

	Sample size	Mean ± SE	Sample range
Primary 10			
Adult males	214	57.34 ± 0.10	53.0–60.8
Adult females	75	53.26 ± 0.11	50.3–57.6
First-year males	66	55.59 ± 0.19	52.2–58.8
First-year females	43	53.13 ± 0.20	49.6–57.7
Primary 8[b]			
Adult males	211	66.86 ± 0.09	62.3–70.7
Adult females	73	62.53 ± 0.13	58.4–64.7
First-year males	66	64.33 ± 0.20	61.1–67.7
First-year females	43	61.90 ± 0.17	56.9–65.1
Tail length			
Adult males	212	58.68 ± 0.09	53.6–62.1
Adult females	75	55.68 ± 0.15	51.7–58.3
First-year males	65	56.70 ± 0.21	53.3–61.4
First-year females	43	54.88 ± 0.19	51.1–58.7

[a]Pooled samples of specimens collected from Alaska to northern Baja California. Details to be presented elsewhere in connection with a systematic revision of the Western Flycatcher (N. K. Johnson, MS).

[b]Equivalent to "wing length" (chord).

by the collector. Specimens of migrants with measurements of primaries 8 and 10 and of tail lengths that fell below the range of values for breeding males and above the range of breeding females, within either age category, were presumed to pertain to the opposite sex and were treated as such in the analysis. This conservative procedure required changing of sex designation for 21 of 264 (=8.0%) specimens of spring migrants.

The figures in Table 1 also are presented to assist the bander in the sexing of live birds whose ages have been determined by plumage criteria.

SPRING MIGRATION ROUTES

The subspecies *E. d. difficilis* of the Western Flycatcher breeds in a linear range along the coast of western North America from southeastern Alaska to northern Baja California, entirely west of the axis of the Sierra Nevada and Cascade Mountains. The principal wintering range of this form, on the tip of Baja California and along the coast of western Mexico from southern Sonora to Oaxaca, also is strongly linear in configuration. The main migratory route in the spring passes directly between the wintering and breeding ranges, through Baja California, western Sonora, southern Arizona, and southern California, then northward through California west of the Sierran divides (Fig. 1). Whether some birds cross the Gulf of

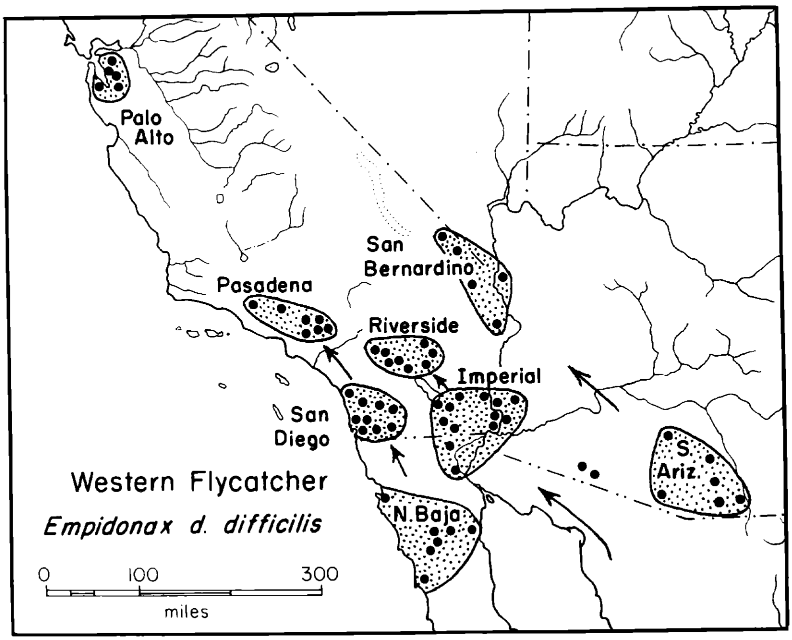

FIGURE 1. Map showing the distribution of the coastal form of the Western Flycatcher in the southwestern United States and Baja California, Mexico during the spring migratory period. Each dot represents the locality of collection of one or more specimens examined for this paper. Specimens were grouped for analysis into the eight named sample areas.

California is conjectural; such movement is not required by the presence of spring migrants in northern Baja California because the latter could represent individuals from the component of birds wintering in the Cape Region of southern Baja California. Records of spring migrants of *E. d. difficilis* from northern Arizona, southern Nevada, and the Mohave Desert of California are scattered. Although this general region has not been collected as intensively for birds as has southern Arizona and southern California, I feel that the relative scarcity of specimens from the northern Mohave Desert is a true reflection of the actual sparse density there and that the bulk of the spring movement of this subspecies passes closer to the continental coast, perhaps through the general area of the lower Colorado River Valley. For the latter region, Grinnell's account (1914: 150) clearly described the abundance of this species as a transient: "First noted April 3 . . . observed almost daily thereafter throughout the trip, the last being seen the day we left, May 15. . . . The migration appeared not to have reached its height until the second week of May when, in the willows of the bottom lands on both sides [of the lower Colorado River] near Pilot Knob, western flycatchers were continually in evidence, through their unmistakable notes."

To facilitate analysis I have divided specimens of spring migrants of *E. d. difficilis* into eight sample areas (Fig. 1) which represent regions of concentration of effort in specimen-collecting within the general zone of northwestward passage of the Western Flycatcher. In Figure 2 I have plotted the collection date of each specimen to show the span of migration of each sex-age group through each sample area. The actual span of migration within any sample area is certainly greater than indicated by specimen records and additional collecting will be required for more precise determination of dates.

The eight sample areas fall into three groups that are situated progressively more interior from the Pacific Coast: I, a "coastal group," including the sample areas of Northern Baja California, San Diego, Pasadena, and Palo Alto; II, a "lower Colorado Desert group," including the sample areas of Imperial and Riverside; and III, an "interior group," including the sample areas in the eastern portion of the migratory front, Southern Arizona and San Bernardino.

In view of the geographic position of Baja California, the preponderance of birds from the northern portion of that state presumably pass through the sample areas of San Diego and Pasadena on their way up the coast. The latter areas, especially Pasadena, probably also receive many transients that have crossed the general region of the lower Colorado River. The comparatively large Imperial sample area includes numerous specimens. This fact, considered with the strategic location of this area, suggests that the great bulk of spring migrants of *E. d. difficilis* pass through the Imperial area after progressing northwestward along the coast and foothills of western Mexico. Unfortunately, no suitable sample exists for comparative study from northwestern or western Sonora. Some birds that pass through the Imperial sample area, especially those from the southern portion in the Colorado River delta, probably then move through the area of San Diego. However, the lateness of mean dates of passage of the sex-age groups through the Imperial area (Tables 2 and 3), when compared with mean dates of

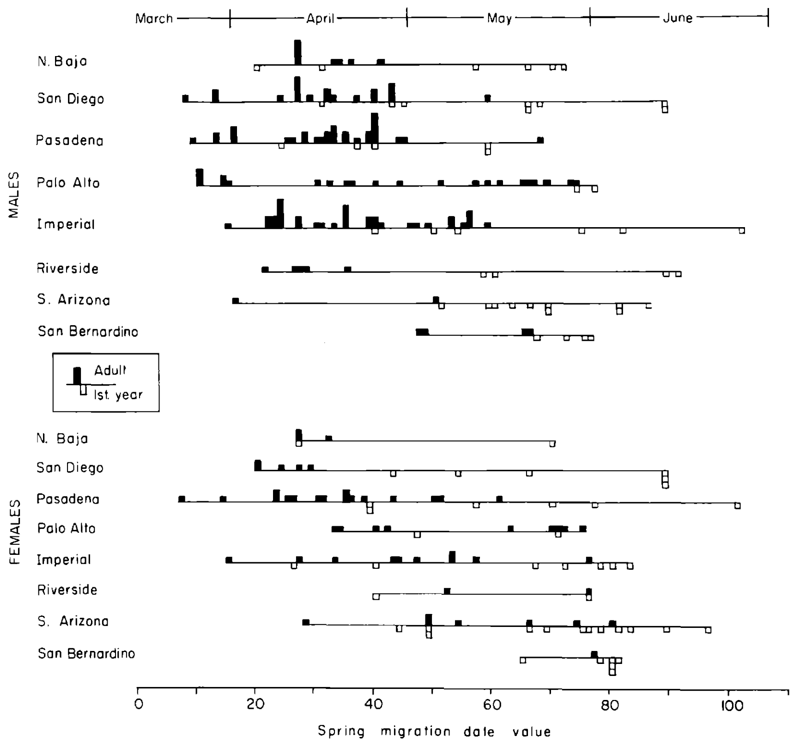

FIGURE 2. Timing of the four sex-age categories of spring migrant Western Flycatchers from sample areas mapped in Figure 1. Each square represents one specimen. See text for explanation of the scale of spring migration date values on the abscissa.

coastal samples (except for the sample of first-year birds from San Diego; Table 3), suggests that at least some of the Imperial birds stay inland, moving through the sample area of Riverside, then progressing northwestward, perhaps over the low passes in theTehachapi Mountains area. The interior sample areas lie near the eastern edge of the general range of spring migration of the coastal race of the Western Flycatcher and probably receive fewer birds in passage than the sample areas of groups I and II to the westward. To the northeast of the areas of group III, *E. d. difficilis* is very scarce in the spring.

A major result of this study is that adults predominate in samples from the coast and lower Colorado Desert, whereas first-year birds are more numerous in the interior samples (Table 3). Of 184 specimens in the combined coastal (Palo Alto excluded) and lower Colorado Desert samples, 132 (= 71.7%) are adult and 52 (= 28.3%) are first-year individuals. The proportions of age groups are reversed in the combined interior samples (Southern Arizona plus San Bernardino) where, of a total of 45 specimens, only 14 (= 31.1%) are adult and 31 (= 68.9%) are first-year birds. These differences are highly significant ($\chi^2 = 25.82$; $P < 0.001$).

TABLE 2. Spring migration date values[a] for Western Flycatchers.

Sample Area[b]	Adult males N	Adult males Mean ± SE	Adult females N	Adult females Mean ± SE	t[c]
N. Baja	8	32.50 ± 1.89	3	29.67 ± 1.67	1.124
San Diego	19	32.42 ± 2.82	5	25.00 ± 1.82	2.215*
Pasadena	30	32.87 ± 2.20	16	34.00 ± 3.48	0.275
Palo Alto	22	43.32 ± 4.92	9	56.44 ± 5.92	1.706
Imperial	34	37.38 ± 2.20	10	45.70 ± 5.39	1.430
	First-year males N	First-year males Mean ± SE	First-year females N	First-year females Mean ± SE	
San Diego	8	63.13 ± 7.48	6	72.67 ± 8.30	0.854
Pasadena	5	44.80 ± 6.76	6	64.83 ± 9.79	1.684
Imperial	6	68.17 ± 9.49	7	64.71 ± 8.32	0.274
S. Arizona	10	69.50 ± 3.53	11	70.64 ± 4.92	0.188
San Bernardino	4	73.50 ± 2.02	6	78.33 ± 2.50	1.504

[a]See the text (p. 205) for the explanation of these values.

[b]The small samples of adults from Southern Arizona, Riverside, and San Bernardino and of first-year birds from Northern Baja, Riverside, and Palo Alto are omitted.

[c]Values of Student's t test resulting from comparisons of sample means of adult males with those of adult females, and of first-year males with first-year females. One instance of significant difference is noted at the 5% level ($P \leq 0.05$) by an asterisk.

TIMING OF THE SPRING MIGRATION

Data derived from dates of specimen collection can be analyzed in two ways when attempting to elucidate sex and age patterns of timing of the spring migratory movement. The first method is to compare the scheduling of each sex and age group *within* each area to see if adult males move in advance of adult females, and so forth. The second method involves comparison of timing of a single sex-age category *among* all sample areas to reveal directional geographic progress with the passage of spring. Ideally, both kinds of analysis require adequate samples of each sex-age group from all sample areas. This is especially true if subtle differences in scheduling are to be demonstrated. In the present study this requirement is satisfied only partially; additional collecting in several areas will be necessary to clarify more fully the spring migration in this common species. Of the sample areas outlined here, additional specimens are needed most from Northern Baja California, Riverside, and San Bernardino. Beyond this general area, samples of spring migrants from northwestern Mexico and from western California north of the Pasadena region would be most useful.

Comparative timing of spring migration by sex-age categories within sample areas.—Preliminary comparison of adult males with females within each of several samples suggests that either no differences in scheduling exist between these categories or that subtle differences

TABLE 3. Migration date values[a] for age groups of the Western Flycatcher.

Spring migration		Adults			First-year birds		
Sample Area	N	Per cent adult	Mean ± SE	N	Per cent first-year	Mean ± SE	t[b]
N. Baja	11	57.9	31.73 ± 1.46	8	42.1	52.63 ± 7.74	2.652*
San Diego	24	63.2	30.88 ± 2.33	14	36.8	67.21 ± 5.51	6.079***
Pasadena	46	80.7	33.26 ± 1.86	11	19.3	55.73 ± 6.66	3.249**
Palo Alto	31	88.6	47.13 ± 3.99	4	11.4	68.25 ± 6.86	2.662*
Imperial	44	77.2	39.28 ± 2.13	13	22.8	66.31 ± 6.02	4.237***
Riverside	7	53.8	38.86 ± 7.41	6	46.2	70.00 ± 8.12	2.835*
S. Arizona	9	30.0	52.78 ± 6.83	21	70.0	70.10 ± 3.01	2.320*
San Bernardino	5	33.3	61.60 ± 5.75	10	66.7	76.40 ± 1.80	2.456*
Fall migration		Adults-First-year birds			Juveniles		
Pasadena	7	16.3	27.86 ± 7.22	36	83.7	55.25 ± 3.46	3.420**
Riverside	8	44.4	37.00 ± 2.05	10	55.6	52.50 ± 3.57	3.762**
San Diego + Imperial	0	—	—	14	100.0	69.64 ± 2.84	—

[a]See the text (p. 205) for the explanation of these values.

[b]Values of Student's t test resulting from comparisons of sample means of adults with those of first-year birds, sexes combined. Significant differences are noted at the 5% level ($P \leq 0.05$) by one asterisk, at the 1% level ($P \leq 0.01$) by two asterisks, or at the .1% level ($P \leq 0.001$) by three asterisks.

do exist but that the numbers of specimens are insufficient to demonstrate these differences statistically (Table 2). The latter alternative is probably the correct one although it is puzzling that in the single instance in which the sexes of adults are different at a statistically meaningful level (San Diego sample area), the direction of difference is contrary to expectation, with the small sample of adult females apparently migrating ahead of many of the adult males.

Within first-year birds, no differences are apparent in timing of males and of females passing through the same sample area. Such differences might exist but the large variances of migration date values of first-year birds require larger samples than those currently available if differences are to be shown. Interestingly, in the single largest sample of first-year birds (21 individuals from Southern Arizona), the mean migration date values of males and females are very similar (Table 2). But even this sample is insufficient in size.

Although the data do not demonstrate sexual differences in scheduling during the spring migration, when age groups are compared, striking differences are observed. In Figure 2, adults average earlier in timing than first-year birds for all samples of males and for all but two samples of females. Statistical analysis of migration date values, when sexes are combined in a comparison of age groups (Table 3), shows that the differences in scheduling are significant for all sample areas. Differences in average timing between adults and first-year birds are greater in the samples from the coast and Colorado Desert (three to five weeks) than in those from the interior (two weeks).

Inter-area comparisons of scheduling.—Along the coast of southern California the Western Flycatcher passes northward between the last week of March and early May, with a peak in mid-April. Migration through the sample areas of group II (Imperial and Riverside) is similar in duration, but shifted somewhat later, peaking late in the third week of April. Spring movement through Southern Arizona is protracted, from late March through the third week of June, but the peak is much later (6 May for adults and 24 May for first-year birds) than the peaks of samples taken nearer the coast. The restricted span of passage, from early May to early June, through the sample area of San Bernardino, might be in part an artifact of insufficient early spring collecting in that area. Nonetheless, the specimen records from there indicate migration that spans a minimum of one month. It is important to note that both the first-year birds and adults pass through the sample areas of groups I (Palo Alto excluded) and II earlier than through the areas of group III in the interior. But the greatest difference in timing among all sample areas is less for first-year birds (24 days; N. Baja versus San Bernardino) than for the adults, in which the most different coastal and interior samples (San Diego versus San Bernardino) peak approximately one month apart (Table 3). The lateness of passage of the Western Flycatcher through the interior, therefore is not solely a result of the preponderance there of first-year birds.

Mean time of passage of adult males through Palo Alto is in late April, approximately 10 days later than through Pasadena, located approximately 250 miles to the southeast. In contrast, the adult females seem to time the peak of spring migration through Palo Alto on about 10 May, or almost three weeks later than through Pasadena. This difference between the sexes, although of marginal statistical significance ($P = 0.10$), suggests a more rapid northward migration of males than of females, once the general southern edge of the breeding range is reached, a point which deserves further study. Data from Ralph (1968), on spring migration of the Western Flycatcher at Bolinas, Marin County, only 40 miles north of Palo Alto (from where most of the specimens were taken which represent the Palo Alto sample area), indicate that the bulk of the birds pass through between mid-April and mid-May. Such timing of passage through Bolinas accords well with that of the entire Palo Alto sample (Fig. 2). Unfortunately, because Ralph's sample was unsegregated by sex or age and was grouped into two-week periods for presentation, more precise statements on comparative scheduling, between Bolinas and Palo Alto, are not possible at this time.

In summary, the data point to an early northwestward migration of substantial numbers of birds across the lower Colorado Desert and up the coast of southern California, a movement which starts in late March and continues in diminishing numbers until late May, and a lesser and predominantly later spring passage of birds through the interior, across southern Arizona and through the northern Colorado and Mohave deserts.

NOTES ON THE AUTUMN MIGRATION

Although the number of specimens is inadequate at this time to support a detailed analysis of fall migration in the Western Flycatcher, preliminary data from several areas in southern California are pertinent to questions of autumn age ratios and therefore are presented here. Using collection dates of specimens from the sample areas of Pasadena and Riverside, as outlined for the spring migration, I calculated "fall migration date values" on a scale starting on 16 July (= 1) and continuing to 15 October (= 92). These migration date values were then treated statistically to define more precisely the autumn migratory schedules of "adults" (including first-year birds that had just bred) versus juveniles. Significant differences in timing are evident for both sample areas (Table 3); the adults move through each area an estimated two weeks to a month ahead of the juveniles.

For two other sample areas (San Diego and Imperial combined) 14 fall transient juveniles were examined. This combined sample provides a mean date of fall migration of juveniles through southernmost California (Table 3) of 23 September. Thus, the peak of movement of juveniles through the sample areas of San Diego-Imperial is approximately two weeks after the mean date of passage for the combined Pasadena-Riverside sample, which peaks on 8 September. This difference is highly significant ($t = 3.757$; $P < 0.001$).

SEASONAL CHANGES IN SEX AND AGE RATIOS

Mayr (1939), in a classical review of sex ratios in birds, describes pitfalls in the proper determination of ratios for wild species. An especially well-documented example of sex ratio determination in grackles (*Cassidix*) has been presented by Selander (1960, 1961). He demonstrated clearly how faulty methodology had led to publication by another worker of erroneous sex ratios in this group of birds. For the present research, except for the sources of sampling bias to be mentioned, I have no reason to assume that the representation by sex and age of specimens in museum collections differs substantially from that in nature. Other than a minor difference in size, males and females of migrating and wintering *E. d. difficilis* are identical in appearance and, presumably, in behavior. (Although males may sing rarely on the wintering grounds, the only vocalization delivered during migration, the position note, is given by both sexes.) Age groups likewise are indistinguishable in the field. Therefore, I consider the sex and age composition of my total sample of 229 specimens of spring migrants from the southwestern United States and northern Baja California, Mexico, to be representative of the true proportions of these categories in natural populations of the Western Flycatcher at that season. In the analysis to follow I compare these spring ratios of sex and age classes with data on proportions of the various categories at other times of the year (Table 4) in an attempt to detect seasonal patterns of change.

TABLE 4. Sex and age ratios in the Western Flycatcher.[a]

Season	N	Per cent males	Per cent females	Per cent adult	Per cent subadult[b]
Spring migration	229[c]	63.3	36.7	63.8	36.2
Breeding areas	398	70.4[d]	29.6	72.6	27.4
Fall migration	121	54.5	45.5	18.2	81.8[e]
Wintering areas	152	59.9	40.1	57.9	42.1

[a]For the subspecies *E. d. difficilis,* which breeds along the north temperate Pacific Coast.

[b]"Subadult" for the spring migration and for the breeding season refers to first-year individuals. For the fall migratory period, "subadult" pertains only to the juveniles hatched that year; the category of adults would include all individuals that had just bred—both the adults and the first-year birds that migrate south before the postnuptial molt.

[c]Sample from Palo Alto excluded.

[d]The sex ratios of breeding birds are undoubtedly biased toward males; see the text (p. 214) for discussion.

[e]The age ratios of fall migrants are probably biased toward subadults; see the text (p. 216) for discussion.

Sex ratio.—Information on the sex ratio at the time of fertilization (primary sex ratio) is unavailable for any flycatcher, and data on sex ratios of nestlings (secondary sex ratio) apparently have not been published for any species of *Empidonax.* For the Western Flycatcher, the earliest ontogenetic stage at which my data permit calculation of the secondary sex ratio is that represented by a sample of fall transient juveniles. Admittedly, this "secondary" ratio might have changed from the true secondary sex ratio at hatching, but in the absence of data on ratios in nestling birds, the ratio in fledged juveniles a few months removed from the nest is offered as the closest approximation now possible to the actual secondary sex ratio. Of 99 specimens of fall transients examined, 53 are males and 46 are females, providing a sex ratio of 53.5% males to 46.5% females. Although this ratio does not differ significantly from 50:50 ($\chi^2 = 0.494$; $P = 0.50$) it agrees surprisingly well in magnitude and direction with the sex ratio calculated for a much larger sample of 409 fall juvenile-immature specimens of the Hammond Flycatcher (*Empidonax hammondii*), which is composed of 57.5% males and 42.5% females (N. K. Johnson, MS), and which does differ significantly from 50:50 ($\chi^2 = 9.098$; $P < 0.005$). A large fall sample might demonstrate a sex ratio in the Western Flycatcher that also is significantly unbalanced toward males, but on the basis of evidence presently available I must assume that the sex ratio of fall transient juveniles in this species is 50:50.

However, during the winter period the sex ratio is definitely not 50:50; a sample of 152 winter specimens of *E. d. difficilis* is composed of 59.9% males and 40.1% females. There is no evidence of a partial geographic segregation of the sexes in winter, thus resulting in sampling bias during this period. The sex ratio during the spring migration is even more unbalanced (63.3% males to 36.7% females), and suggests that in some manner the females are less able to cope with the rigors of migration. The relative increase in the proportion of males continues into the breeding season, although for this period some if not all of the difference in sex ratios, when compared with that of the spring migration period, is the result of bias toward males, one which occurs during sampling of nesting populations. In my experience, the greater ease of collecting singing males versus incubating or brooding females on the nesting grounds suggests that some of the imbalance in the sex ratio of breeding birds in this species certainly is a result of sampling bias. Even after consideration of this bias, however, data from other seasons strongly suggest that the breeding sex ratio in this species is on the order of 65% males to 35% females.

In the Hammond Flycatcher the data indicate a similar increase in the proportion of males to females through the winter and spring months. For the latter season, a sample of 160 specimens from southern Arizona shows a ratio of 64.4% males to 35.6% females (Johnson, 1965: 427), figures which are nearly identical to those for spring migrant samples of the Western Flycatcher (Table 4).

The reason for the imbalanced adult (tertiary) sex ratio in these flycatchers is not readily apparent, but until the issue is clarified by further data I speculate that a combination of subtle factors, one of which is increased mortality of females during migration and especially during incubation and brooding, operate differentially on the sexes to reduce the average survival of females. Mayr (1939) provides examples of this phenomenon for other species of birds.

Age ratio.—The number of birds that have bred (adults and first-year individuals) when compared to the number of juveniles of the year, in a sample of 121 fall migrants from southern California and Arizona, reveals a strikingly high percentage of young birds (81.8%). Banders in central coastal California at the Point Reyes Bird Observatory, Marin County, also report very high ratios of young to adult birds among fall migrants of *E. d. difficilis* (Ralph, 1968). For example, Stewart (1971: 5) and colleagues banded 175 young, but no adult, Western Flycatchers during the fall migration of 1971 at Bolinas, California. Although relatively large numbers of juveniles are to be expected during the fall period, immediately after the reproductive season, the scarcity or absence of adults requires explanation.

Ralph (1968) has proposed that young birds concentrate along the coast because their orientation capabilities are less precise or less developed than those of adults. Although this reason might account for some of the imbalance in age ratio, I do not think that differential routes of the fall migration by age groups is the entire answer to the problem because the fall specimens here analyzed (from the southwest) represent all geographic portions of the migratory front, and yet adults still are scarce in the samples. Instead, the timing and perhaps the speed of the fall movement of adults might result in a false impression of scarcity during the "normal" period of migration, when in fact many or most of the adults might have already migrated by the time the bulk of the young birds pass through in the last of August and the first half of September. From preliminary data given above, and as I demonstrate elsewhere (Johnson, 1974), adults of the coastal form of the Western Flycatcher migrate south very early; some individuals are already on the wintering grounds in Mexico by early August, long before the arrival of the first juveniles. This implies a substantial southward movement of adults even in July, a point which receives support from Ralph's (1968) report of an influx of adults in July into his study area at the Point Reyes Bird Observatory.

By the time the wintering grounds are reached the proportion of young in the population is strikingly reduced from that of the fall migration, from 81.8% (although this figure is admittedly too high; see above) to 42.1%. Presumably this reflects the tremendous impact of differential mortality of young versus adults during the fall migratory period, a situation also seen clearly in *Empidonax hammondii* (Johnson, 1970: 175). In addition, as L. R. Mewaldt (pers. comm.) suggests, the fact of earlier arrival of adults on the wintering grounds might permit their pre-emption of the best territories for survival at that season, resulting in increased mortality of the later arriving young. There is further apparent decline of the component of young from 42.1% in winter, to 36.2% in spring migration, to 27.4% during the breeding season (Table 4). This might result from increased mortality of relatively inexperienced first-year birds faced with the hazards of their initial northward migration. Additional differentially increased mortality of first-year birds could also occur after arrival on the breeding grounds as a result of competition for breeding space with older birds that have previously held territories.

DISCUSSION

The new data for the Western Flycatcher invite comparison with information published earlier for the Hammond Flycatcher (Johnson, 1965, 1970), a congeneric species that also migrates overland in great numbers through the southwestern United States. During the spring migration of both species, the adults favor the more coastal routes and the first-year birds move predominantly through the interior. For *E.d. difficilis*, the coastal route definitely provides the most direct access between the geographically closest portions of the linear breeding and wintering areas. Because the more easterly interior route emphasized by the subadults is less direct than that chosen by the majority of the adults, and because in general the young birds show greater geographic scatter during migration than do the older birds, I speculate that at least some young birds have imperfect orientation mechanisms. The broad dispersion of subadults during the late spring passage across the lowlands and foothills of the southwest must be costly to the species in terms of increased mortality and reduced total breeding effort. Although many of these first-year birds probably return to the general region of their birthplace, some also might represent pioneers, potential colonists to previously unoccupied habitat, and as such, fulfill a significant evolutionary role.

Although it is generally assumed for passerine birds that the majority of the adult males migrate ahead of the adult females in the spring (Dorst, 1963: 252), proper documentation for this phenomenon is lacking for most species of migratory birds. Nolan and Mumford (1965: 328) present convincing evidence that differential timing of the sexes, with the adult males leading, is indeed the case for the Prairie Warbler (*Dendroica discolor discolor*). Similar data are available for the White-crowned Sparrow (King et al., 1965). In the present analysis, except for the sample areas of San Diego and probably Palo Alto, the sexes seem to pass essentially in synchrony, within each age group, through each sample area. This contrasts with the situation in *E. hammondii*, in which the bulk of the males move ahead of the peak of females. Larger samples, obtained at regular intervals of time and from representative portions of the migratory front, are needed to clarify this point in *E. difficilis*; specimens in collections are still insufficient for certain periods of time and for particular areas.

Preliminary findings for the fall movement of the Western Flycatcher point to a strongly asynchronous passage of age groups, with the mass of adults moving ahead of the juveniles through at least two areas of southern California. The sexes within each age group seem to migrate in synchrony. Again we see a difference in data from the Hammond Flycatcher in which all four sex-age classes seem to peak at approximately the same time when passing through a given region. That pronounced interspecific differences exist should not be surprising, for intraspecific variation in the timing relationships af age groups moving through two geographic regions has recently been demonstrated for the Least Flycatcher (*Empidonax minimus*). At Long Point, Ontario, this species shows differential scheduling of age groups in the fall, with most adults preceding the majority of the young (Hussell et al., 1967). Approximately 170 air miles SSE of Long Point, near Rector, Westmoreland County, Pennsylvania, both age classes pass through the westernmost valley of the Allegheny Mountains at approximately the same time in the fall (Clench, 1969). Clearly, the temporal and geographic complexities of migration in *Empidonax* are only beginning to be unraveled. We should anticipate numerous further differences, even between very closely related species and among populations of the same species, differences concerned most directly with specific adaptive patterns (Tordoff and Mengel, 1956: 40; Johnson, 1970: 183).

The Western Flycatcher, which along the Pacific Coast of North America is one of the more easily identified and the most abundant species of *Empidonax*, deserves more attention from students of migration than it has received heretofore. The fact that age groups can be distinguished in the spring places the species into a very select category in terms of research potential. Although research opportunities on *Empidonax* still are considerable for banders using traditional techniques, several problems persist of which I will stress only one. The proper determination of sex of live birds often is not attempted (Hussell et al., 1967; Ralph, 1968; Clench, 1969; Stewart, 1971), and the lack of migratory data that are segregated by sex continues to impede research in this genus. The continued overreliance on wing length data for sex determination is to be discouraged; overlap between the sexes in this character is substantial (Table 1) and the difficulty of proper measurement of living birds in the field results in values that are unrefined and approximate at best. More dependable data will derive from birds that have been sexed by laparotomy or by dissection prior to preservation as study specimens. Such skins then can be aged in the museum by detailed examination of plumage, their identifications can be checked by careful measurement, and they are available for study by future workers. The Western Flycatcher in particular lends itself to this approach. As a species which occupies a vast range where breeding populations are moderately dense and reproductive rates high, large samples of migrants could be preserved for study to great advantage.

A final cautionary note is in order. As I demonstrate elsewhere (Johnson, 1974), an unexpectedly high proportion (approximately 85%) of *breeding* Western Flycatchers possess non-pneumatized areas in the roof of the skull. The presence of these "windows" in both first-year birds and in adults beyond the first year renders questionable age determination by this means in this species at any season. Reliance on plumage characters for the separation of age groups continues to be appropriate.

SUMMARY

Data from 264 specimens of the coastal form of the Western Flycatcher (*Empidonax difficilis difficilis*) demonstrate differential timing and routes of sex and age categories during the spring migration in the southwestern United States and northern Baja California, Mexico. Most spring migrants apparently move directly northwestward from the wintering range along the coast of western Mexico, up the coast and foothills of western Sonora, across the lower Colorado River Valley, and through the coastal region of California. Statistical analysis of collection dates of specimens permitted quantitative appraisal of scheduling of movement. The sexes appear to migrate in synchrony in the spring, in contrast to the migration of the Hammond Flycatcher in which the majority of the adult males usually precede the females. In common with the latter species, adults of the Western Flycatcher predominate in an early movement near the coast and lower Colorado River Valley; subadults comprise the majority of individuals in a later, more interior movement through southeastern Arizona and the northern Colorado and Mohave deserts. Within a sample area, adults are from two to five weeks ahead of first-year birds in average date of peak migration.

Preliminary information for the autumn migration points to a rapid passage of adults in the late summer, overlapping with a later, more prolonged southeasterly movement of juveniles.

Comparison of seasonal sex and age ratios in the total sample of spring migrants, plus 671 additional specimens from other seasons, indicates a sex ratio of 50:50 in fall juveniles, a ratio which gradually changes through the winter and spring to a ratio of approximately 65% males to 35% females during the breeding season. A pronounced change in the age ratio after each migration apparently results from differentially heavy mortality of relatively inexperienced young.

Comments are offered on the current program of research on migration in *Empidonax*. Improved methodology of sex and age determination of live birds at banding stations and additional widespread sampling of specimens of migrants are important continuing needs.

ACKNOWLEDGMENTS

In addition to the extensive material in the Museum of Vertebrate Zoology, specimens were examined from the following sources: Dickey Collection at the University of California, Los Angeles (courtesy of Thomas R. Howell and James G. Miller); California Academy of Sciences, including the Stanford University Collection (courtesy of Robert T. Orr and Laurence C. Binford); San Diego Society of Natural History Museum (courtesy of Joseph R. Jehl); University of Kansas Museum of Natural History (courtesy of Robert M. Mengel); Philadelphia Academy of Natural Sciences (courtesy of James Bond); Los Angeles County Museum (courtesy of Kenneth E. Stager and James R. Northern); American Museum of Natural History (courtesy of Dean Amadon and Wesley E. Lanyon); and Moore Laboratory of Zoology at Occidental College (courtesy of John William Hardy). I sincerely appreciate the kind assistance of these curators in permitting me to examine material in their care and for numerous other courtesies during my visits to their institutions. L. Richard Mewaldt and Sue Kaiser read the manuscript and offered beneficial suggestions.

Final versions of the illustrations were prepared by Gene M. Christman and the manuscript was typed by Mrs. John G. O'Connor.

Partial assistance for travel expenses and for handling specimens was provided by the National Science Foundation (Grant GB-3834).

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Received 1 March 1973, accepted 15 May 1973.