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FALL MIGRATION AND WINTER DISTRIBUTION OF THE HAMMOND FLYCATCHER

By NED K. JOHNSON

In connection with a general investigation of the biology of several species of flycatchers in the genus *Empidonax* (Johnson, 1963a, 1963b, 1965, 1966), I examined autumn and winter specimens of the Hammond Flycatcher (*Empidonax hammondii*) available in the major American and Canadian museums. Although the routes of autumn migration and regions of winter occurrence of this species are known in a general way, certain of the previously published information is either questionable or erroneous owing to the difficulty of specimen identification in the genus *Empidonax* (Miller, *et al.* 1957: 86, footnote). With the development of refined techniques of ageing and criteria of specific identification (Johnson, 1963a), many of the problematical specimens have been determined, including all of the series of *hammondii* described incorrectly by Moore (1940) as hybrids of *hammondii* and "*wrighti*" (= *Empidonax oberholseri*, the Dusky Flycatcher). There has been no previous attempt to survey in detail the fall migration of the Hammond Flycatcher. Furthermore, using specimens of known age it is possible now to investigate the timing of the autumn movement through the western United States to detect possible differences based on age or sex as was done earlier (Johnson, 1965) for the spring migration of this species. The recent paper by Hussell *et al.* (1967) on differential fall migration of age groups in the closely related Least Flycatcher (*Empidonax minimus*) in Ontario provides a useful comparative study.

METHODS AND MATERIALS

For the present analysis 236 specimens of fall migrants of the Hammond Flycatcher were examined from British Columbia, the western United States, and extreme northern Mexico. For investigation of both fall and spring migration in the remainder of Mexico and in Central America, 208 skins were studied. An additional 200 specimens taken in the period from November 1 through February 28 provided information on winter distribution. Therefore this study is based on a total of 644 museum specimens.

As in my survey of differential timing and routes of the spring migration in this species, collection dates of specimens were converted to "migration date values" which permitted statistical treatment of timing of migration. Autumn migration was considered to fall in the period of August 1 through October 31. Each month is valued at 30 units; the scale is 90 units long. Thus, a specimen taken on August 21 has a migration date value of "21", one taken on September 20 a value of "50", and so on. For August and October, 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 figure 2 to equate particular migration date values with actual autumn dates.

Except for minor differences in size the Hammond Flycatcher is sexually monomorphic and there are no features by which age groups can be distinguished in the field. Therefore it is assumed that examples of the various sex-age groups were collected without bias, that is, according to their availability in the environment, and that museum specimens accurately reflect the proportions of the different categories present in the field at the time of sampling.

BACKGROUND INFORMATION ON DISTRIBUTION AND TIMING OF FALL MIGRATION

Statements in the literature based on verifiable specimens provide only a very general picture of the autumn migration of the Hammond Flycatcher. In the state of Washington, Jewett *et al.* (1953: 426-427) record the species as late as September 22. The latest date for Oregon is September 23 (Gabrielson and Jewett, 1940: 395-396). In the northwestern United States where *hammondii* breeds commonly it is difficult to determine with precision the timing of the onset of migration because birds passing southward in the early fall from northern regions (British Columbia, for example) are mixed imperceptibly with late summer residents. In California, where the species breeds in mountainous regions in the northern part of the state and southward through the Sierra Nevada, Grinnell and Miller (1944: 257-258) state that, "Birds in passage either way appear on both sides of Sierran axis, but to westward seem mostly to avoid the immediate coast belt." They write further that "Fall migration south through lowlands is not so conspicuous as spring migration, but it is seemingly more protracted." They give no specific dates for the fall movement. Their comment about the existence of a post-breeding "up-mountain" movement of *hammondii* to as high as 10,500 feet in the Sierra Nevada is to my knowledge not based on any conclusive evidence. Since no marking studies have been done to demonstrate that the birds found at high altitudes indeed were derived from downslope breeding populations, one could also interpret these records as representing birds resident to the north which are passing south along the crest of the Sierra Nevada during fall migration. In Joshua Tree National Monument in southern California, Miller and Stebbins (1964) record *hammondii* from October 13 to 23. They remark further that the migration probably also occurs earlier but that the species was not taken in considerable collecting of *Empidonax* flycatchers in August and early September.

Autumn movement through the interior of the western United States is very poorly understood. There is no dependable published information for fall migration of *hammondii* in either Idaho or Wyoming. In Nevada there are a few published specimen records of *hammondii* in the fall from September 2 to 22 (Linsdale, 1936: 76-77). All of the specimens documenting these records are in the Museum of Vertebrate Zoology and their identifications have been corroborated. In his check-list of the birds of Utah, Behle (1944: 77) lists the Hammond Flycatcher only as a summer resident. Woodbury *et al.* (1949: 20) record *hammondii* to as late as September 19 in Utah. In three other papers Behle (1943, 1958, and 1960) includes records of fall migrants from several mountain ranges in Utah which span dates from August 16 through September 18. Dr. Behle has kindly permitted me to examine large series of *Empidonax,* including the specimens from the studies mentioned above, which have resulted from his field work in Utah. In Appendix A I have listed the localities in Utah represented by the autumn *hammondii* among the specimens I have identified. To the east in Colorado, Bailey and Niedrach (1965: 526) record the species as late as September 19; no other fall records are given.

A specimen in the Philadelphia Academy of Sciences (Number 35449), which apparently has been overlooked by previous investigators, establishes the very early occurrence of the Hammond Flycatcher at "Clear Creek, Kansas Territory." This skin, taken by W. S. Wood, Jr. in "July, 1859," may have been an early fall transient. The Kansas State Historical Society lists no fewer than 14 "Clear Creeks" from within the current boundaries of Kansas (*fide* Carla Bowman), thus I am unable to place the locality more precisely. There are two additional fall specimens from Kansas reported recently by Ely (1968: 89), both from the vicinity of Hays in Ellis County. They bear dates of September 15, 1961, and October 4, 1966. I have not had the opportunity to verify the identifications of these individuals. According to Sutton (1967: 345-346) *hammondii* passes through Oklahoma as a fall transient with definite records occurring from September 18 to October 2. The only identifications I have been able to substantiate for Oklahoma are those of the four skins taken at six miles south of Kenton between September 21 and 26 (Sutton, 1934).

Fall records for New Mexico as compiled by Bailey and Cooke (1928: 437-438) are difficult to evaluate because they seem to be contaminated by those of other species. These authors report *hammondii* from August 25 to September 30, although a July 30 record from near Willis is given which could well represent a summer resident. If a specimen exists to document this report I have not seen it. Ligon (1961: 183-194) simply repeats selected records from Bailey and Cooke. For Texas, Wolfe (1956: 47) records *hammondii* as a spring and fall migrant in the southwestern part of the state. More specific fall data, from the Guadalupe Mountains of Texas, are provided by Burleigh and Lowery (1940: 111) who state, "In early October the Hammond flycatcher was found not only to

Figure 1. — Map showing the distribution of *Empidonax hammondii* in western North America in the late summer and fall. Each symbol represents the locality of collection of one or more museum specimens. The dots represent birds in molt, through postnuptial molt stage 6 and through postjuvenal molt stage 4 (see Johnson [1963a: 124-128] for definition of molt stages). Note that all of the dots are enclosed by the heavy line which delimits the principal breeding range of the species. Half shaded symbols represent specimens in late phases of the fall molt and in fall migration. Circles represent specimens of birds in fall migration, all of which had completed the fall molt; these are the specimens which form the basis for the analysis. Shaded areas (A - F) include samples examined for differences in timing of the fall movement by the various sex and age groups.

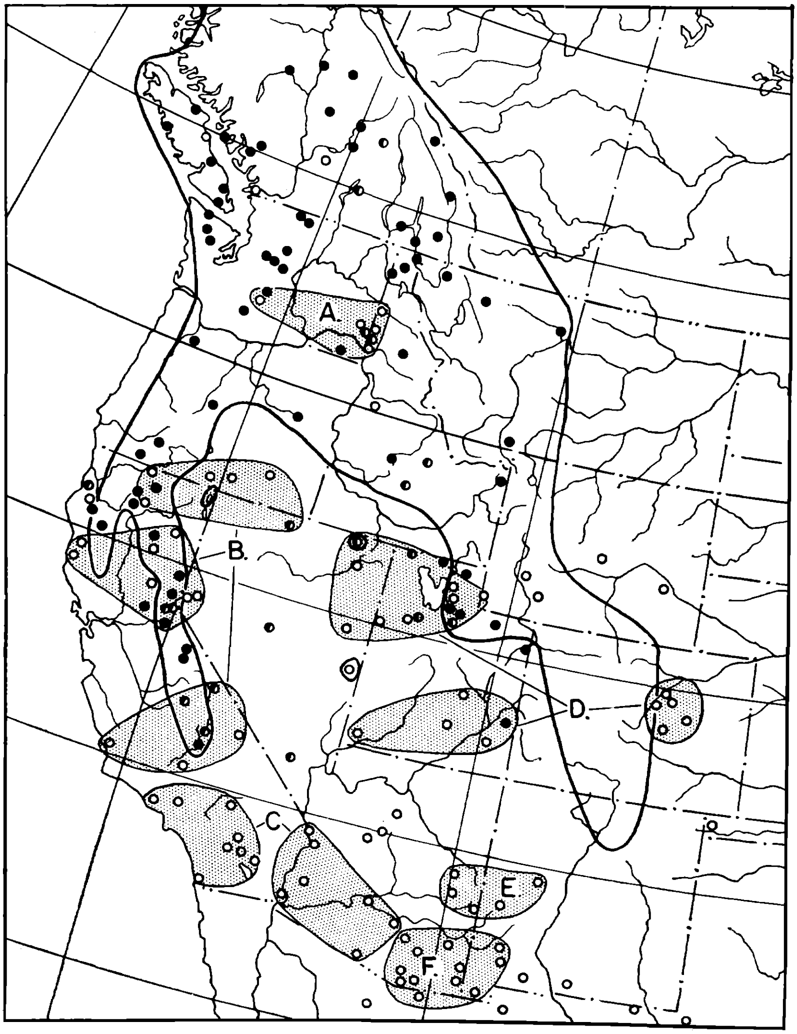
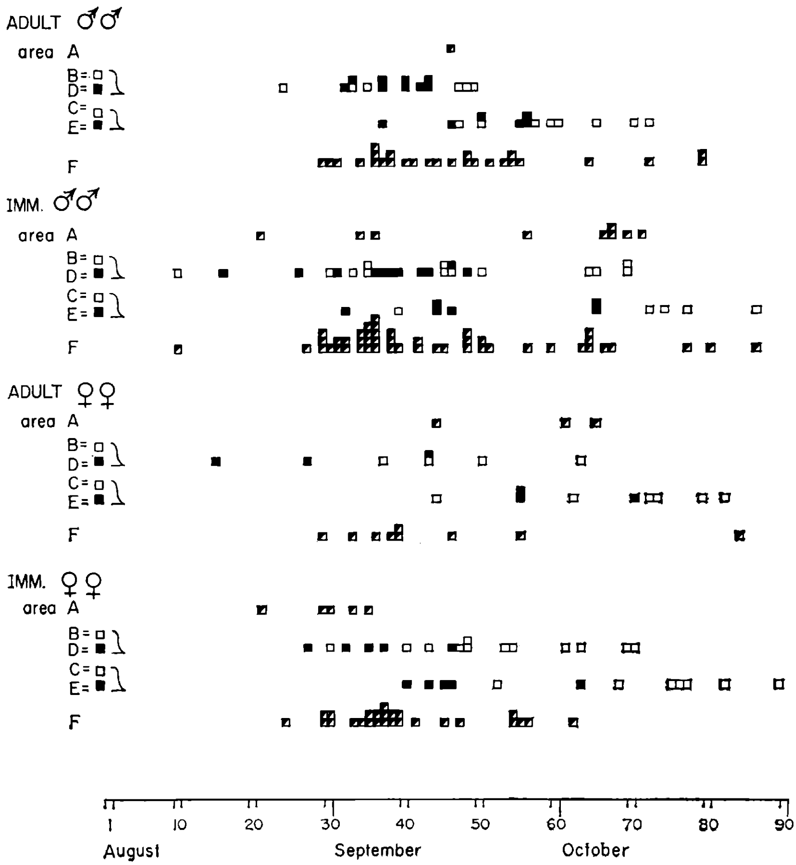


Figure 2. — Timing of four sex-age categories of specimens of fall migrant Hammond Flycatchers from sample areas mapped in figure 1. Each square represents an individual bird. See text page 170 for explanation of the numerical scale at the lower edge.



be fairly common, but apparently the only species of this genus then present in this region . . ."

For northern Arizona, Phillips *et al.* (1964: 87) state that the span of fall migration is from August 22 to October 15. For southern Arizona and extreme northern Sonora their records fall from August 11 to November 4. The specimen taken on the latter date may have been a winter visitor. van Rossem (1945: 158) records the species as a fairly common fall migrant through the mountainous eastern part of Sonora, with dates extending from August 11 to October 15.

ROUTES OF THE FALL MIGRATION

The circles in figure 1 represent birds which had completed the fall molt or birds which were collected in the autumn at localities outside the known breeding range. A list of the localities mapped in figure 1 is provided (Appendix A). These specimens were grouped into a number of sample areas (shaded on map) for comparison. After initial study revealed that some of the areas were represented by too few specimens for meaningful analysis, certain areas were combined in order to increase sample size. Thus, Area B consists of three regions originally studied separately, Area C of two regions, and Area D of three regions. Hopefully, collecting in the future will permit the more refined study made possible by examination and comparison of large samples from more restricted geographic regions. In any event the present comparatively gross survey allows one to contrast fall movement through the more coastal regions of California and southwestern Arizona (Areas B and C) with migration through more interior regions of northeastern Nevada, Utah, and Colorado (Area D), and eastern Arizona and western New Mexico (Area E). Migration in these broad regions can then be compared with movement through southeastern Arizona and southwestern New Mexico (Area F).

As would be expected for this boreal species, birds in the fall move southwardly mostly along the mountains, such as the Sierra Nevada, before crossing the Pacific slope of southern California and the southwestern deserts. Records from the northern and central Pacific Coast and Great Valley of California are scarce or lacking, as are records from the Great Basin. Records of fall migrants from the Rocky Mountains region are scattered both in time and space, making interpretation difficult.

The proportions of the four sex-age groups in the sample from Area F in southeastern Arizona and southwestern New Mexico (table 1) may represent a reasonably accurate appraisal of these proportions in the entire population of transients passing through the southwest in the fall for the following reasons: (a) Area F is situated geographically so as to intercept the probable center of the migratory front entering Mexico from the United States; (b) this sample is the largest (109 specimens) of any considered here; and (c) this sample spans the longest period (77 days) of the fall migration of any sample. However, the proportions in Area F deviate at a highly significant level from those in the sample of 200 specimens from the winter range ($\chi^2 = 60.54$; 3 d. f.; $p < 0.01$). As I have indicated previously (Johnson, 1965: 425) winter and spring ratios are very similar and do not differ statistically. That the autumn proportions of the four sex-age groups apparently differ from those of winter and spring should not be surprising; the data indicate a striking decline in the immature component (table 2) of both sexes and suggest that increased mortality of young versus adults is a basic population change in the late fall and early winter. Table 2 further shows that the sex ratio, in contrast to the age ratio, does not change significantly between fall and winter.

TABLE 1. COMPOSITION OF SAMPLES OF HAMMOND FLYCATCHERS

Sample Area	N	Adult No.	Males %	Imm. No.	Males %	Adult No.	Females %	Imm. No.	Females %
Fall Migrants									
A	18	1	5.5	9	50.0	3	16.7	5	27.8
B	35	6	17.1	13	37.2	4	11.4	12	34.3
C	26	8	30.8	5	19.2	6	23.1	7	26.9
D	28	9	32.1	11	39.3	3	10.7	5	17.9
E	20	6	30.0	6	30.0	3	15.0	5	25.0
F	109	27	24.8	47	43.1	9	8.3	26	23.8
B+C+D+E	109	29	26.6	35	32.1	16	14.7	29	26.6
North of Area F	159	35	22.0	52	32.7	23	14.5	49	30.8
Winter Range	200	94	47.0	35	17.5	41	20.5	30	15.0
Spring Migrants[1]	160	68	42.5	35	21.9	29	18.1	28	17.5

[1]Data from Sample Area 2 only (Johnson, 1965: 427), which is comparable in geographic position to Sample Area F of the present study.

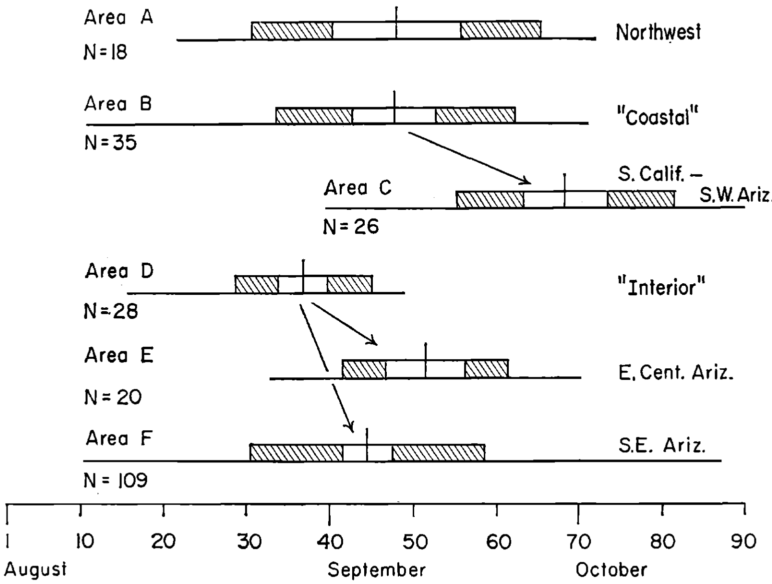
The validity of the proportions from Area F may be checked by contrasting them with proportions in populations to the north (table 1). First, a summation of all fall migrants (159 specimens) taken north of Area F, compared with the sex-age composition of samples from Area F, shows that although the proportions in the samples are remarkably similar they differ at marginal statistical significance ($\chi^2 = 9.52$; 3 d. f.; $p < 0.05$). A more refined comparison of birds from Area F with samples from Areas B through E summed (109 specimens; birds from Area A are excluded because of the

TABLE 2. SEX AND AGE RATIOS IN THE HAMMOND FLYCATCHER

Season	N	Per Cent Males	Per Cent Females	Per Cent Adult	Per Cent Imm.
Fall Migration					
Areas B through E	109	58.7	41.3	41.3	58.7
Area F	109	67.9	32.1	33.3	66.7
Winter	200	64.5	35.5	67.5	32.5
Spring Migration[1]	160	64.4	35.6	60.6	39.4

[1]Data from Sample Area Number 2 in southeastern Arizona (Johnson, 1965: 427).

Figure 3. — Comparative timing of fall migration between sample areas. Within each sample area, all sex-age categories are combined. Horizontal line denotes sample range, vertical line denotes sample mean. The clear rectangles indicate two standard errors on each side of the mean; the patterned rectangles extend for one standard deviation on each side of the mean. Statistics calculated from migration date values; the latter are explained on page 170 Scale of migration date values is shown at bottom of figure.



possibility that this sample includes late residents as well as migrants) yields results nearly identical with those of the first comparison ($\chi^2 = 8.20$; $p < 0.05$), and which values are also at inconclusive levels of statistical significance. However, both comparisons show that the sex-age proportions of samples from Area F are generally similar to those of populations to the north and, except for the adult females which seem to deviate significantly, I assume that the proportions of sex-age groups in samples from Area F rather closely approximate the true proportions in nature.

A comparison of sex-age composition of samples between the various geographic regions reveals no clear picture of differential routes of migration in the fall as was found earlier for the spring migration.

TIMING AND SPEED OF THE FALL MIGRATION

Two diagrams are presented to assist in the interpretation of data on timing and speed of the autumn movement. In figure 2 are compared individuals of the same sex and age category, but from different sample areas. Note especially the differences between "coastal" (Areas B and C) and "interior" (Areas D and E) specimen

TABLE 3. FALL MIGRATION DATE VALUES[1] FOR THE HAMMOND FLYCATCHER

Sample Area[2]	Number of Specimens	Sample Range	Mean with Standard Error	Standard Deviation
A	18	22–72	48.28 ± 4.21	17.36
B	35	11–71	48.17 ± 2.41	14.04
C	26	40–90	68.65 ± 2.61	13.03
D	28	16–49	37.11 ± 1.56	8.09
E	20	33–71	51.65 ± 2.26	9.86
F	109	11–87	44.68 ± 1.35	14.05

[1]See page 170 for an explanation of the derivation of these values.
[2]All sex and age groups combined.

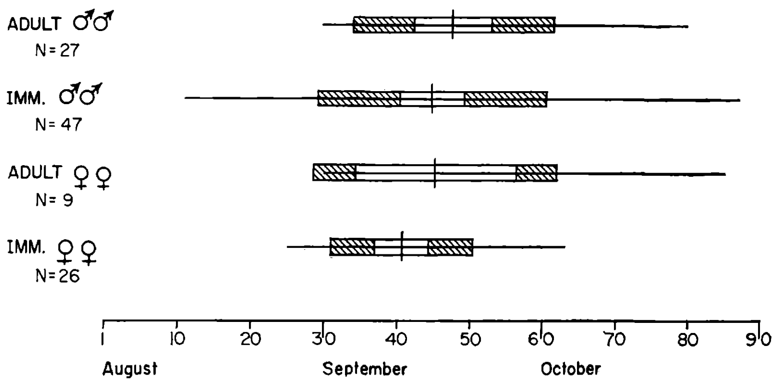
dates, which are contrasted by the use of open squares versus black squares. In figure 3 specimens of all sex and age categories are combined to allow comparison of timing of migration of the species as a whole between the different sample areas. The actual migration date values are given in table 3. Note the standard deviations of the timing of migration in table 3. Preston (1966) has calculated similar standard deviations for the timing of certain migrants in eastern North America and has arrived at figures in the general order of five to ten days. His standard deviations are comparable in length to those of several areas studied in the present paper. Preston's paper thoroughly explores the complexities of patterns of timing in different species and describes them in mathematical terms.

Area A.—All five of the immature females are ahead of the three adult females. The combined span of these two groups is essentially the same as that of the immature males. Only one adult male is available and there is the possibility that birds of that category had already departed. No conclusions are warranted from these sparse data. The span of migration through Area A by the species (all sex-age groups combined) is approximately seven weeks, from the last one-third of August through the first third of October.

Area B.—The immature males, adult females, and immature females all occur during about the same period, from late August through the first third of October, although one immature male is dated August 10(?). Adult males seem to move through Area B about a week earlier than the other groups, on the average, although only six records are at hand to document this supposition. The span of migration through Area B by the species as a whole is over seven weeks.

Area C.—All sex-age groups pass through this area at roughly the same period, from mid-September to late October, hence the

Figure 4. — Statistical representation of timing of migration of the four sex-age groups through Area F in southeastern Arizona and southwestern New Mexico. See legend to figure 3 for the explanation of the diagram.



peak is approximately two to three weeks later than that for Area B to the north. The span of migration through Area C is approximately seven weeks.

Area D.—Birds of all sex-age groups pass through this area from mid-August to the third week in September, therefore spanning a five-week period. No obvious differences in peaks of timing are apparent from the rather small samples of the groups, although it seems that the adults have slightly more restricted spans of passage than do the immatures.

Area E.—Migrants occur in this area over a span of over five weeks, from early September through the first third of October. All sex-age categories apparently pass through at about the same time, although samples are small.

Area F.—This sample of meaningful size (109 specimens) spans nine weeks of the fall migration period, from late August through October, exclusive of a single August 11 record of an immature male. See figure 4 for a statistical analysis of this sample, which shows that the bulk of all sex-age groups pass through in September. A more rapid passage of immature females than of other categories is suggested, but not proved, by the sample of that group at hand. An exploratory plotting of all sex and age groups combined revealed no evidence of bimodality, although the curve is rather strongly skewed (see Area F in figure 3) toward the right, that is, toward the later period of the fall migration. Some of the very late birds may actually be wintering and not migrant individuals; they would help skew the curve. Specimens from this area may be spread temporally for two reasons: (1) the sample is large and therefore a broad representation of dates is to be expected, and (2) the sample is from an area placed rather far south and thus migrants are intercepted from rather diverse sources to the north.

WINTER DISTRIBUTION

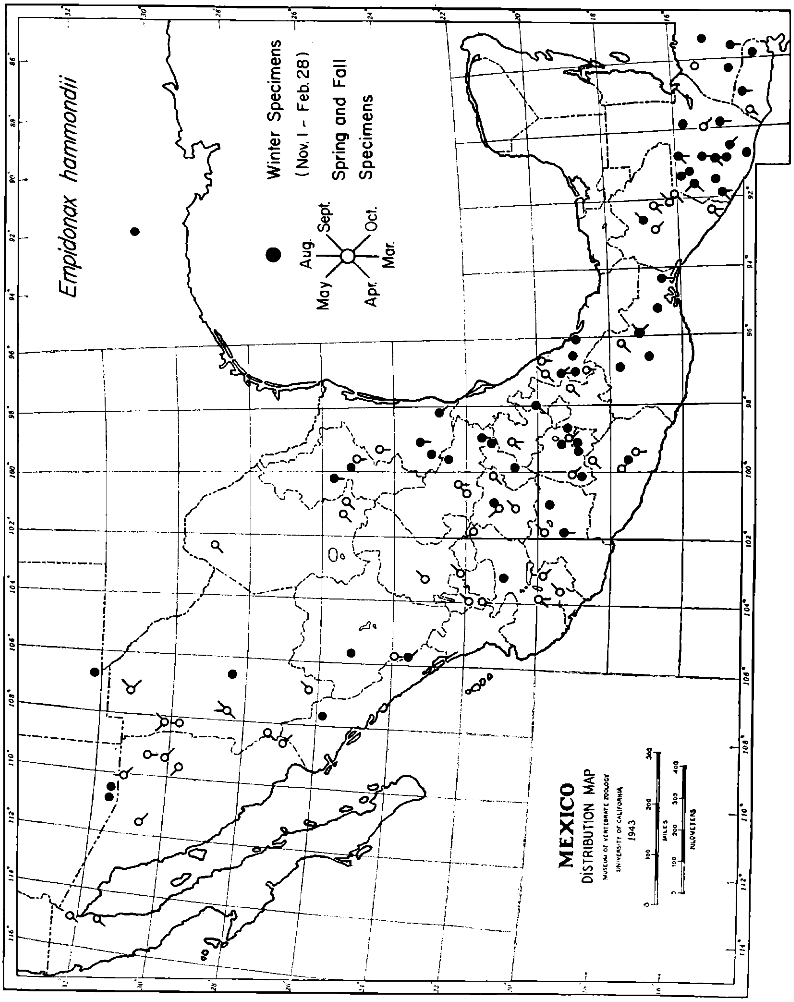
The northern limits of the winter range are not well documented. In Appendix B are listed the localities represented by specimens I have examined with dates between November 1 and February 28. An exceptional first-year male (Chicago Natural History Museum No. 140923) taken on March 19, 1921, at Thermal, Riverside County, California is included also with the winter residents because of the early date and because it was taken in the midst of a heavy pre-nuptial molt. On the basis of data from many other specimens this molt always occurs on the wintering grounds prior to the spring movement (Johnson, 1963b). This specimen was not listed by Grinnell and Miller (1944: 257-258, although they do include the record by Tyler (1920: 190) of a male taken in the bottomlands of the Merced River near Livingston, Merced County, on December 20, 1918. I have been unable to locate this specimen to substantiate the identification. There seem to be no other winter occurrences of the Hammond Flycatcher in California.

Additional winter specimens from the United States have been taken in Pennsylvania (Heintzelman, 1968: 512), Louisiana (Lowery, 1960: 365), New Mexico (Appendix B), and Arizona. I have examined winter specimens from two localities in the latter state. Phillips *et al.* (1964) state that this species winters regularly near Patagonia and they list additional records from "near Phoenix," the Chiricahua Mountains, and Salome. I have not had the opportunity to examine the specimens from the latter localities to verify their identifications.

These authors overlooked the December 4, 1904, specimen which was taken by H. Kimball in the Huachuca Mountains (Museum of Comparative Zoology number 303583).

The map of winter distribution and localities of migration in Mexico and Central America (figure 5) lacks symbols for the winter birds mentioned above from California and from Pennsylvania, both of which were examined after the map was prepared. At the present state of our knowledge the records from Louisiana and Pennsylvania are best classed as winter vagrants. Winter occurrence of the Hammond Flycatcher is irregular in California. From southeastern Arizona and extreme southern New Mexico, southward well into Mexico, winter records increase in number, although there are vast regions where specimens are lacking and regularity of winter occurrence is not yet established. Much of this region has not been well collected by ornithologists, especially during the winter. Very likely the species winters regularly through both the Sierra Madre Occidental and Sierra Madre Oriental from at least southern Chihuahua and central Nuevo Leon southward. As stated in Miller *et al.* (1957: 88) there are no records from the tropical lowlands; although a few specimens represent foothill localities, most are from medium or high elevations on major mountain systems. At the southern end of the known winter range in Honduras, *hammondii* also winters mostly in the highlands, occurring between mid-October and mid-April (Monroe, 1968: 267-268). This

Figure 5. — Distribution of migrant and wintering Hammond Flycatchers in the southern United States, Mexico, and Central America. Each symbol represents the locality of collection of one or more museum specimens examined by the author.



broad span of winter residence demonstrates the conservativeness of the November through February period used as the basis for definition of winter specimens in this paper.

I have not seen specimens from Nicaragua to substantiate the statements in Eisenmann (1955) and Miller *et al.* (1957) that *hammondii* occurs in that country, although the species would be expected to winter in the northern highlands. Also I have seen no specimen from Peru and cannot verify the occurrence there mentioned in Miller *et al.* (*loc. cit.*). Meyer de Schauensee and Eisenmann (1966) do not list the Hammond Flycatcher from any country in South America.

DISCUSSION AND CONCLUSIONS

Geographic variation in timing and routes of fall migrant Hammond Flycatchers. — Tentatively, several significant conclusions are suggested by the data. Birds moving through Washington and central California span approximately seven weeks, migrating through the first third of October. These birds apparently then pass through southern California and southwestern Arizona, two to three weeks later, into late October. In contrast, migrants from the interior in Utah and Colorado pass through over a period of only five weeks, to the third week in September. These birds apparently then pass through the general area of eastern Arizona and western New Mexico two weeks later and through the first third of October. The large sample of 109 specimens from southeastern Arizona and southwestern New Mexico, spanning nine weeks from late August through October, doubtless includes birds from both coastal and interior routes. Because of the late peaking of coastal movement, it is likely that the bulk of the late migrants through southeastern Arizona are from the coastal source. Similarly, the earlier interior migrants probably constitute a significant proportion of the earlier birds passing through Area F in the fall.

As in the spring migration birds from western North America seem to funnel through southeastern Arizona and southwestern New Mexico during the fall movement. To the west, the Hammond Flycatcher apparently skips Baja California and western Sonora on the way south, and, to the east, birds are scarcer toward eastern New Mexico and western Texas. Admittedly, this funnelling effect could be accounted for partly by regional differences in amount of collecting. The western and eastern sections of the total migratory front certainly have not received the collecting effort comparable to that devoted in the past to the mountains of southeastern Arizona. However, the differences in numbers of specimens between these areas are too great to be accounted for entirely by degree of collecting. Some notion of the abundance of *hammondii* moving through southeastern Arizona may be gained from the statement of Phillips *et al.* (1964: 87) that "the observer must be impressed with the great numbers of small migrant flycatchers in woodlands throughout much of the state, and he may take comfort in the knowledge that most of them are Hammond's. Occasionally Hammond's gives a call nearly as sharp as that of a Pine Nuthatch, thus identifying itself. During some migrations, the woods at middle elevations of the mountains resound with these single *peeps*."

Differences between migrations in spring and fall.—In the spring migration of this species, an early rapid migration in coastal regions contrasts with a protracted movement northward through the interior (Johnson, 1965). An opposite pattern is shown by the fall movement, in which there is a leisurely migration through coastal areas compared to an early and comparatively rapid passage southward from the interior. In my opinion these differences between coastal and interior migrants definitely are adaptive, although the selective forces promoting the adaptations are obscurely understood. I speculate that favorable conditions for migration, in terms of food abundance and moderate temperatures, persist longer in the late autumn in the southwestern United States than in the interior. Furthermore, in the autumn passage there may be no advantage for the emphasis on different routes by sex and age groups as was indicated for adult males and first-year females in the northward spring passage.

Timing of sex-age classes within one region.—Although several of the samples are small, the present data indicate that the mass of each of the four sex and age groups pass through each region at approximately the same time. This finding of synchrony, at least in southeastern Arizona if not in all areas, contrasts strongly with reports on the fall movement of the Least Flycatcher in Ontario (Hussell, *et al.*, *op. cit.*) in which species the mass of the adults precedes the immatures by several weeks. Larger samples of Hammond Flycatchers might well reveal subtle differences in timing not clarified by the present analysis. However, it is unlikely that the magnitude of such possible differences would approach those found between the age groups of the Least Flycatcher. A point of speculation is that synchrony of timing of movement of the sex-age classes may increase as the birds go farther south. If so, samples of fall migrant Least Flycatchers from more southerly localities might show a picture different from that obtained in Ontario.

Differential timing of sex and age classes of birds in general.—Since the useful review by Tordoff and Mengel (1956) which points out the complexity of differential fall migration, additional data have been published for a variety of species. Important recent studies, for example, have dealt with *Limnodromus griseus* (Jehl, 1963), *Larus minutus* (Knötzsch, 1964), *Parus caeruleus* and *Parus major* (Jablonski, 1965), *Hylocichla* (Annan, 1962), *Dendroica discolor* (Nolan and Mumford, 1965), *Dendroica caerulescens* (Hubbard, 1965), *Fringilla coelebs* (Deelder, 1949; Schifferli, 1963; Dobrynina, 1963; Dolnik and Blyumenthal, 1967), and *Zonotrichia leucophrys* (King, *et al.*, 1965). The paper by Krüger (1938), which includes significant data on differential migration in *Turdus* *viscivorus* and *Turdus torquatus*, seems to have been overlooked by most recent authors. Murray's excellent paper (1966) presents original data for a number of species and reviews the pitfalls inherent in interpretations of information on differential migration. He concludes from an examination of species of passerines in autumn movement that in eastern North America, (1) adults and immatures travel at approximately the same time; (2) there is no evidence that immatures travel separately from adults; and (3) of 44 species examined, only the Red-eyed Vireo (*Vireo olivaceus*) clearly shows an overlapping asynchronous pattern of migration, with overlap in the timing of movement of adults and immatures but with a shift in the ratio of adults to immatures.

It is not the purpose of this paper to analyze in detail the foregoing literature. However, one significant point emerges from these investigations of numerous kinds of birds; that is, the great variation in timing and routes by different sex and age classes within the various species precludes broad generalization. In other words we may expect to find differences even between closely related species that are concerned most intimately with their specific adaptations and evolution, and that at the present state of research in this area it is improper to invoke explanations which cover birds in general. We can best return to the suggestion of Tordoff and Mengel (*op. cit.*: 40) "that explanations of these patterns may be sought in the life histories of the species involved."

Points of more general ecologic relevance may also be raised by investigations of timing of movement of sex and age classes. Selander (1966: 140) has included differential migration of the sexes as a form of ecologic polymorphism which could function in the alleviation of competition within a species. Especially during the autumn migration when species populations are at annual peaks one might assume that competition could be significant and that selection would favor the temporal spacing of individuals so as to reduce their impact on the food resources. Because a significant number of species demonstrate synchronous timing of age groups in fall migration, at least on the basis of currently available evidence, it may be that competition is not a serious general problem. However, it is likely that for some species there is initial antagonism and eventual compromise between spacing of age groups so as to avoid competition and synchrony so as to facilitate orientation and movement southward of inexperienced young. The autumn migration is a rigorous event for a species, especially the young individuals (witness fall mortality of young as indicated indirectly in table 2), and if synchrony with adults pays off in increased survival, this synchrony would have a high selective value.

In conclusion I would like to repeat my earlier plea (Johnson, 1965: 435-436) to banders that they preserve for study any banded *Empidonax* flycatcher they recover, even those found at a short distance from the site of original marking. Reliable information on the migrations of birds of this difficult genus will accumulate only when specimens are saved as vouchers of the specific identification of the individual birds involved.

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SUMMARY

This paper analyzes timing and routes of the autumn migration and winter distribution of the Hammond Flycatcher (*Empidonax hammondii*) from data provided by 644 museum specimens of known identity, sex, and age—the only source of verifiable information for birds of this genus. Maps and lists of precise localities of occurrence for fall migrants and winter residents are provided.

When the total specimens of fall migrants are divided into six geographic subsamples, several trends are evident. This species passes southward through northern and central California over a seven week period, which peaks in mid-September. Two to three weeks later the bulk of these birds migrate through southern California and southwestern Arizona, into late October. In contrast, the migrants from the interior in Utah and Colorado span only five weeks, with a peak in early September. The mass of these birds then passes southward through eastern Arizona and western New Mex-

ico. Birds from both of these general regions, the "coast" and the "interior", apparently then funnel through southeastern Arizona and southwestern New Mexico; the total migration there spans a nine week period, from late August through October. Because of the differences in timing between migrants passing along the coastal and interior routes, it is probable that the bulk of the early migrants in southeastern Arizona are from the interior and that the bulk of the later migrants are from the coastal source.

Although several samples are small, the present data indicate that the four sex and age categories migrate essentially in synchrony through each region in the fall. This finding contrasts with the asynchronous autumn passage through Ontario of age groups of the closely related Least Flycatcher.

Differences in age composition between autumn and winter samples point to a comparatively high mortality of immatures in the late fall and early winter.

Museum of Vertebrate Zoology and Department of Zoology, University of California, Berkeley, California 94720.

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APPENDIX A

Fall Specimen Localities Mapped in Figure 1

CANADA

BRITISH COLUMBIA. *Prince Rupert District*: Dease Lake; New Hazelton. *Vancouver Island*: Comox.

UNITED STATES

WASHINGTON. *Yakima County*: 3 mi. NE Bumping Lake at Goose Prairie; S Fork Tieton River. *Whitman County*: 3 mi. NE Albion; 2 mi. NW Pullman; "Rose at 4 mi. Cks." *Asotin County*: Saddle Butte.

OREGON. *Grant County*: 12 mi. SSE John Day. *Lake County*: Hart Mt.; Old Fort Warner. *Harney County*: Krumbo Creek.

CALIFORNIA. *Siskiyou County*: Beswick; McCloud. *Lassen County*: Eagle Lake, 4200 feet. *Mendocino County*: Sherwood; Lierly's. *Trinity County*: 8 mi. NE Hyampom, 2900 feet. *Nevada County*: Soda Springs; Grass Valley. *Butte County*: Jonesville. *Eldorado County*: Angora Lake, 7000 feet; Lake Audrain, 7300 feet; Echo. *Inyo County*: Wyman Creek, 6000 feet, White Mts.; Cottonwood Lakes, 11000 feet, Sierra Nevada Mts. *Fresno County*: Hume, 5300 feet. *Los Angeles County*: Pasadena; Roscoe; Mt. Wilson, San Gabriel Range. *Kern County*: Thompson Canyon, 3900 feet, Walker Basin. *San Bernardino County*: Oro Grande; San Bernardino Mts. *San Luis Obispo County*: San Luis Obispo. *San Diego County*: San Diego. *Riverside County*: Strawberry Valley, San Jacinto Mts.; Pinyon Wells, 4000 feet; Cottonwood Spring, 3000 feet. *County Unspecified*: "Kern River."

IDAHO. *Custer County*: Loon Creek Ranger Station, 6000 feet. *Kootenai County*: 8 mi. NE Ford. *Latah County*: Moscow; Potlach. *Nez Perce County*: Lewiston. *Valley County*: McCall.

WYOMING. *Converse County*: Douglas. *Uinta County*: 14 mi. N Evanston, 7000 feet, Bear River Divide. *Natrona County*: Rattlesnake Mts., 7500 feet. *Sweetwater County*: Green River; Rock Springs.

NEVADA. *Humboldt County*: Martin Creek Ranger Station, 7000 feet, Santa Rosa Mts. *Washoe County*: Third Creek, 7800 feet, 3/4 mi. S and 1 mi. W Incline Lake, Carson Range; Thomas Creek, 6000 feet, Carson Range. *Elko County*: Bear Creek, 8000 feet, Jarbidge Mts; Camp 23, E Humboldt Mts. (= Ruby Mts.). *Storey County*: Six Mile Canyon, 5200 feet. *White Pine County*: Lehman Creek, 7000 feet, Snake Mts. *Lander County*: Kingston Creek, 8000 feet.

Clark County: Lee Canyon, 9000 feet, Charleston Mts.; Hidden Forest, 8500 feet, Sheep Mts.

UTAH. *Weber County*: 3-1/2 mi. NW Ogden; Ogden. *Boxelder County*: Raft River Mts. *Tooele County*: Clover Creek, 5800 feet, 3 mi. W Clover. *Salt Lake County*: Silver Lake P. O. (Brighton), 8500 feet. *Juab County*: Summit Deep Creek Mts. near Ibapah Peak, 10000 feet. *Washington County*: Near Whipple Valley, 9000 feet, 5 mi. E Pine Valley, Pine Valley Mts. *San Juan County*: Geyser Pass, 10000 feet, La Sal Mts.

COLORADO. *El Paso County*: 2 mi. N Peyton. *Adams County*: Bar, 20 mi. E Denver, 6000 feet; Denver. *Lincoln County*: Big Sandy Creek at Limon. *Adams County*: Bennett. *County Unspecified*: Navajo Creek (= Navajo River, Archuleta County?).

ARIZONA. *Coconino County*: Oak Creek; Sedona; 9 mi. NW Flagstaff at Fort Valley, 7200 feet. *Pima County*: Happy Valley, 6 mi. N Mescal, SE side Rincon Mts.; Sycamore Canyon, W slope Baboquivari Mts.; Thomas Cañon, 4500 feet, E side Baboquivari Mts.; Tucson; Santa Catalina Mts. *Yuma County*: Bill Williams Delta, Havasu Lake National Wildlife Refuge; 3 mi. W Hoodoo Well, Kofa Mts.; Wilbanks Cabin, Kofa Mts.; 1 mi. NNW Tunnel Springs, Kofa Mts.; Owl Woods, Imperial National Wildlife Refuge. *Cochise County*: Head of Ramsey Canyon, Huachuca Mts.; Portal, Chiricahua Mts.; Palmerlee; Apache; Paradise. *Santa Cruz County*: Madera Canyon, Santa Rita Mts; 3 mi. SW Patagonia, 4000 feet. *Graham County*: "near Mt. Graham." *Yavapai County*: 10 mi. W Prescott. *Greenlee County*: Blue River, 6000 feet. *County Unspecified*: "Gila River"; "near Forestdale."

NEW MEXICO. *Catron County*: Reserve. *Socorro County*: Gallinas Mts., 7500 feet. *Luna County*: Florida Mts. *Hidalgo County*: W side San Luis Mts., Mexican Boundary Line. *Dona Ana County*: 3 mi. W Las Cruces, 3800 feet. *Grant County*: Apache; Hachita; Burro Mts.

OKLAHOMA. *Cimarron County*: 6 mi. S Kenton. (Not "Kenton" as labelled. See Sutton, 1934: 37).

TEXAS. *Ward County*: Monahans. *Culberson County*: Guadalupe Mts.—Pine Springs Canyon, 5800 feet; McKittrick Canyon, 6000 feet.

KANSAS. *County Unspecified*: Clear Creek.

MEXICO

SONORA. Rancho Carrizal, N of Altar; Las Cuevas; San Jose Mts.

CHIHUAHUA. Lake Santa Maria; Colonia Pacheco; Meadow Valley, 5 mi. S Garcia, 7500 feet.

APPENDIX B

Winter Specimen Localities

UNITED STATES

ARIZONA. *Cochise County*: Huachuca Mts. *Santa Cruz County*: 2 mi. SW Patagonia.

CALIFORNIA. *Riverside County*: Thermal. (Collected on March 19, 1921; see text page 000).

LOUISIANA. *Rapides Parish*: Woodworth, 10 mi. S Alexandria.

NEW MEXICO. *Dona Ana County*: 1 mi. S Mesilla Dam, 3900 feet.

PENNSYLVANIA. *Lehigh County*: near Schnecksville (not plotted in figure 5).

MEXICO

CHIAPAS. 5 mi. S Ciudad Las Casas, 7000 feet; Geneta Mts.

CHIHUAHUA. Carmen.

GUANAJUATO. Rancho Enmedio, 17 mi. NE from Guanajuato, 6000 feet.

GUERRERO. Chilpancingo.

JALISCO. Guadalajara, Barranca de Portillo.

MEXICO. Amecameca, 9000 feet; Contreras; Temascaltepec, 5500 feet.

MICHOACAN. 5 mi. SW Ario de Rosales, 5000 feet; El Temazcal, 20 mi. E Morelia, 7300 feet; Lagunita, 13 mi. NE Ario de Rosales, 7000 feet; km. 291, 21 km. by road E Morelia, 6800 feet; Rancho Los Ates, 5 mi. W Ario de Rosales, 5500 feet; Sierra de Ozumatlan, 33 mi. W Hidalgo.

MORELOS. Cerro Cuauteptl, Lagunas de Zempoala Natl. Park, 3000 m.; Huitzilac.

NUEVO LEON. El Blanquillo, 8 mi. NW Montemorelos, 1500 feet; Monterrey; 2 - 3 mi. N Monterrey.

OAXACA. Cerro San Felipe, 6500 feet; Chivela; Llano Verde, 45 mi. NW Oaxaca, 7000 feet; Moctum [= Moctun, about 5 km. ESE Totontepec].

PUEBLA. 30 mi. E Huachienango, 1200 feet; Scopa, 3 mi. NE Huachienango, 4000 feet.

QUERETARO. El Caracal [= El Caracol?], 5 mi. NW San Juan del Rio, 5900 feet.

SAN LUIS POTOSI. Agua Zarca Region, 2.3 mi. by highway E Agua Zarca, 3900 feet; Alvarez; C. Maiz (15 mi. E); Pendencia Region, 1.5 mi. S village, 4300 feet; 10 km. E Platanito; San Miguel Region, 4 mi. SW Puentede Dios [= Puente de Dios?]; Xilitla Region, 1 mi. WSW village [and many other localities around village], 2400 feet.

SINALOA. Babizos, 6400 feet; El Batel, 70 km. NE Mazatlan, 5100 feet; Palos Verdes Mine, 1 mi. E Santa Lucia, 3900 feet; Rancho Batel, 5 mi. N Santa Lucia, 5200 feet.

TAMAULIPAS. Victoria.

VERA CRUZ. Mirador, near Vera Cruz; Orizaba; Puente de Guadalupe, 9 mi. S Huatusco, 4300 feet.

GUATEMALA

ALTA VERA PAZ. Finca Sepacuite [= 50 mi. E Coban].

CHIMALTENANGO. Canderas [= Calderas?], NW slope Volcan de Acatenango, 7600 feet; Tecpam [= Tecpan, Texpan], Sierra Sta. Elena; Sta. Elene [= Sta. Elena?], 8500 feet.

GUATEMALA. Mixco, 7000 feet.

HUEHUETENANGO. Barrillos; Chanquejelve; Huehuetenango; San Juan Ixcoy, about 2200 feet; San Mateo.

JALAPA. Finca San Francisco Bellavista, Jalapa, 4500 feet.

QUEZALTENANGO. Quezaltenango [= Quetzaltenango].

QUICHE. Chichicastenango; Finca El Soche [= 20 mi. E Uspantan]; Uspantan [= Uspanlan?].

SAN MARCOS. V. Tajumulco, San Marcos, 6000 feet.

SOLOLA. Rio Panajachel, Panajachel, 5300 feet; San Lucas.

TOTONICAPAN [= Totonicapam]. Momostenango.

ZACAPA. Zacapa, 8 mi. NW Usumatlan [= Usumatan?], 6200 feet.

EL SALVADOR

CHALATENANGO. Los Esesmiles, 8700 feet; San Jose del Sacare, 3600 feet.

MORAZON. N slope Mt. Cacaguatique, 4600 feet.

SAN MIGUEL. Mt. Cacaguatique, 3500 feet.

HONDURAS

MOSQUITIA. Intibuca, Esperanza, 5400 feet; Intibuca, 4 mi. SE Esperanza, 5900 feet.

TEGUCIGALPA. Alto Cantoral; Cerro Cantoral; D. C.: 1 mi. NW Zambreno; Monte Redondo.

YORO. Portillo Grande, Yoro, 4000 feet.

ADDITIONAL NOTES ON THE FLYCATCHERS OF EASTERN NORTH AMERICA

By Allan R. Phillips and Wesley E. Lanyon

Banders and, to some extent, museum workers have apparently found the paper by Phillips, Howe, and Lanyon (1966) to be a useful guide to the identification of flycatchers, particularly the genus *Empidonax*, in eastern North America. When the need for a third printing developed this year, it was suggested that we might wish to incorporate new data and perhaps make corrections in the original text before reprinting. To avoid possible bibliographic problems, we recommended that the 1966 paper be reprinted in its original form and that any further remarks appear in this supplement. Our principal objectives here are to provide a more comprehensive treatment of the five western species of *Empidonax* that were not included in the 1966 key, to add another *Myiarchus* flycatcher for consideration by eastern banders, to clarify the status of certain tyrannids in Florida, particularly southern Florida, and to comment further on the general problems of flycatcher identification that continue to plague banders. Our discussion of such problems has been prompted by correspondence and conversations with a