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FALL MIGRATIONS OF ALDER AND WILLOW FLYCATCHERS IN SOUTHERN ONTARIO

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Abstract.—Adult Willow Flycatchers (*Empidonax traillii*) and Alder Flycatchers (*E. alnorum*) occurred earlier than immatures in fall migration at Long Point, Ontario, by an average of 15 and 14 d, respectively. Both adult and immature Willow Flycatchers migrated significantly earlier in fall than the same age classes of Alder Flycatchers. Fall migration of adults of the two species spanned almost the same period (third week of July to fourth week of August) but there was a preponderance of Willow Flycatchers early in the period and Alder Flycatchers later, resulting in median dates of occurrence of 8 and 14 August, respectively. Most immature Willow Flycatchers occurred from the second week of August through the first week of September, but immature Alder Flyctachers tended to start migrating about a week later and median dates of occurrence of immatures of the two species were 23 and 28 August, respectively. Adults molt the flight feathers in the winter quarters, but nearly all adults and many immatures of both species were molting body feathers during fall migration.

The timing of migration and molt in adult and immature Willow and Alder Flycatchers followed similar patterns to those of Least Flycatchers (*E. minimus*) and Yellow-bellied Flycatchers (*E. flaviventris*), but adult Least Flycatchers migrated an average of 2–3 wk earlier than the other species, both spring and fall (Hussell 1981, 1982b). Adults of the four species spent 64–72 d on the breeding grounds. Immatures of the four species migrated together, on average 14–38 d later than adults of their own species, and occurred almost simultaneously except that immature Willow Flycatchers were 5–6 d earlier than the immatures of the other species.

MIGRACIÓN OTOÑAL DE *EMPIDONAX TRAILLII* Y *E. ALNORUM* EN EL SUR DE ONTARIO

Sinopsis.—Durante la migración otoñal a través de Long Point, Ontario, los adultos de *Empidonax traillii* y del papamoscas de Alder (*E. alnorum*) llegan 15 y 14 días más temprano que los juveniles de sus respectivas especies. Tanto adultos como inmaduros de *E. traillii* migran significativamente más temprano que individuos de *E. alnorum* de las mismas clases de edad. La migración otoñal de los adultos de ambas especies ocurre virtualmente durante el mismo periodo de tiempo (desde la tercera semana de julio hasta la cuarta semana de agosto) pero hay la tendencia de que *E. traillii* llegue más temprano y la segunda especie más tarde, dando esto como resultado fechas medias de ocurrencia del 8 y 14 de agosto, respectivamente. La mayoría de los inmaduros de *E. traillii* aparecen desde la segunda semana de agosto hasta la primera semana de septiembre, pero los inmaduros del papamosca de Alder tienden a comenzar a migrar una semana más tarde, con fechas medias de partida para ambas especies del 23 y 28 de agosto, respectivamente. Los adultos mudan las plumas de vuelo en los lugares en donde pasan el invierno. Casi todos los adultos, y muchos de los inmaduros de ambas especies, se encontraron mudando las plumas corporales durante la migración otoñal.

El periodo de migración otoñal y la muda en los adultos e inmaduros de las especies antes mencionadas, sigue un patrón similar al de *E. minimus* y *E. flaviventris*, pero *E. minimus* migra un promedio de 2–3 semanas más temprano que las otras especies, tanto en el otoño como en la primavera (Hussell 1981, 1982b). Los adultos de las cuatro especies pasan de 64–72 días en las áreas en donde se reproducen. Los inmaduros de las cuatro especies migran juntos, de 14–38 días (en promedio) más tarde que los adultos de sus respectivas especies, y se encuentran juntos a excepción de los inmaduros de *E. traillii* que llegan de 5–6 días más temprano que las otras especies.

Studies of Least Flycatchers (*Empidonax minimus*) and Yellow-bellied Flycatchers (*E. flaviventris*) at Long Point, Ontario (Hussell 1981, 1982b; Hussell et al. 1967) and elsewhere (Ely 1970; Hussell 1980, 1982a; Johnson 1963; Sealy and Biermann 1983) have demonstrated a pattern that is infrequent among New World passerines. In fall, adults migrate 3–5 wk in advance of immatures, then molt their flight feathers in the winter range. By contrast, most other adult passerine migrants molt the flight feathers prior to southward migration (Dwight 1900) and the age classes migrate essentially simultaneously (Murray 1966).

Two other species in the genus *Empidonax,* the Alder Flycatcher (*E. alnorum*) and the Willow Flycatcher (*E. traillii*) are common migrants in southern Ontario. Their spring migrations at Long Point occur in late May and early June (Hussell 1991). The purpose of this paper is to describe the timing of fall migration of these two morphologically similar species in southern Ontario and to compare their migrations with those of the Least and Yellow-bellied Flycatchers. As before, I will use the name "Traill's Flycatcher" when the two species are considered together or when individuals were not identified as Alder or Willow Flycatchers (Hussell 1991). Fragmentary information indicates that Traill's Flycatchers may be similar to Least and Yellow-bellied Flycatchers in the timing of fall migration of age classes and location of adult flight feather molt (Dwight 1990, Ely 1970, Hussell et al. 1967), but even less is known of the fall migrations and molts of Alder and Willow Flycatchers as separate species (Phillips et al. 1966).

METHODS

Field methods are described briefly here; additional information on *Empidonax* migration studies are in Hussell (1981) and details related to Alder and Willow Flycatchers are in Hussell (1991). Flycatcher migration was studied at the Long Point Bird Observatory's (LPBO) field station at the eastern end of Long Point, on the north shore of Lake Erie in 1966–1968. Each day during the fall migration seasons (1 July–31 October) migrants were captured in Heligoland traps and/or mist nets. In addition, the numbers of each species (and "unindentified" *Empidonax*) present in a defined area (covering approximately the eastern-most 1 km of Long Point) were estimated.

Captured birds were identified, weighed, measured and examined for skull pneumatization and molt as described in Hussell (1991). A sample of birds (usually at least the first five Traill's Flycatchers captured each day in 1967 and 1968 plus a few additional birds in 1966) was examined for body molt, and a composite body molt score with a possible range of 0 (none) to 3 (heavy) was determined. Birds hatched in the current calendar year were called "immatures" while all older birds were "adults." Adult Traill's Flycatchers molt the flight feathers in the winter quarters (Dwight 1900) and experience in this study indicated that this holds for both the Alder and the Willow Flycatchers. After 1 July, birds with worn flight feathers, narrow whitish wing bars and completely or almost com-

pletely pneumatized skulls were classified as adults; those with little or no wear on the flight feathers, broad buffy wing bars and substantially unpneumatized skulls were called immatures. Although the flight feathers of adult Traill's Flycatchers were usually less worn than those of adult Least Flycatchers, most birds were readily aged by plumage criteria alone.

Stein (1963) found that the equation $B = 7.95 + 0.15\ I$ correctly separated an average of about 91% of Willow and Alder Flycatchers. *I*, a measure of wing shape, is (the length of the longest primary minus the length of the sixth primary) minus (the length of the fifth primary minus the length of the tenth primary). Willow Flycatchers tend to have rounder wings (lower *I* values) and longer bills than Alder Flycatchers. *B* is calculated by inserting *I* into the equation. Birds with bill lengths greater than *B* are Willow Flycatchers and those with bill lengths less than *B* are Alder Flycatchers (Hussell 1990, 1991). Stein's equation was derived from adults collected on the breeding grounds and identified to species by song type. Because bills of immatures of several species of *Empidonax* are shorter than those of adults, Stein's equation is probably not accurate for separating immature Alder and Willow Flycatchers (Hussell 1990). Therefore, I used Stein's equation ($B = 7.95 + 0.15\ I$) only for identification of adults and I replaced it with the equation $B' = 7.64 + 0.144\ I$ for identification of immatures (Hussell 1990). Moreover, Stein's equation did not provide complete separation of adults of the two species (Stein 1963), so I attempted to reduce errors by designating as unidentified those adults and immatures whose bill lengths were within 0.15 mm of *B* and *B'*, respectively.

Estimated totals of adult and immature Alder and Willow Flycatchers present in the sampling area each day in the fall were calculated by prorating the daily estimated totals of all identified and unidentified *Empidonax* in proportion to the numbers of each age class of Alder, Willow, Least and Yellow-bellied Flycatchers in the banded samples (Hussell 1981). For this purpose each unidentified Traill's Flycatcher in the banded sample was counted as one-half an Alder Flycatcher and one-half a Willow Flycatcher. Five-day moving averages, medians and percentiles were calculated as described previously (Hussell 1981).

Traill's Flycatchers were banded in 1969–1980 at the same location as the 1966–1968 study (station No. 1) and at a second station (No. 2), 19 km west of station No. 1, in the years 1966–1980, but they were not identified as Alder or Willow Flycatchers. Numbers of these Traill's Flycatchers are presented in the same way as in Hussell (1991) except that data for adults and immatures are given separately.

RESULTS

The sample of 60 trapped adults in 1966–1968 consisted of 24 Willow Flycatchers, 22 Alder Flycatchers and 14 birds that could not be identified to species (see Hussell 1990, Fig. 2, upper). Among 127 immatures, 39 were classified as Willow Flycatchers, 54 as Alder Flycatchers and 34 as unknown (see Hussell 1990, Fig. 2, lower; 2 "unknowns" with incomplete

measurements not shown). Adults clearly preceded immatures in both species (Fig. 1). The distributions by date of trapped Willow and Alder Flycatchers differed significantly both for adults and immatures (Kolmogorov-Smirnov 2-sample tests: $P < 0.05$ and $P < 0.001$, respectively), with Willow Flycatchers tending to occur earlier than Alder Flycatchers (Fig. 1).

Arrival patterns and numbers of adults varied from year to year, but identified individuals of both species were first captured in July in 1967 and 1968 and peak numbers were in the first 3 wk of August. The few adults captured in 1966 (Table 1) were taken on dates ranging from 12 to 24 August. For the 3 yr together, adults of both species showed two peaks: 28 July–1 August and 17–21 August in Willow Flycatchers; 7–11 and 17–21 August in Alder Flycatchers (Fig. 1). The second of these two peaks resulted from exceptional numbers of both species in 1967, particularly on 21 August, when two Willow, three Alder and one unidentified Traill's Flycatcher were captured. This second peak was not confirmed by other banding data, which clearly shows that most migration of adult Traill's Flycatchers is in early August, particularly from 2–11 August (Fig. 2). The largest number of adult Traill's Flycatchers banded on any day was nine at station No. 1 on 7 August 1977, on the same day that the largest concentration of adult Yellow-bellied Flycatchers was recorded there (Hussell 1982b).

Estimated totals indicate that the migration of adults of the two species spanned almost the same period: the middle 90% of Willow Flycatchers in a 38-d period, 17 July–23 August, and Alder Flycatchers in 35 d, 20 July–23 August (Fig. 3, A(T)). A greater proportion of Willow than Alder Flycatchers migrated early, however, resulting in median dates for estimated totals on 8 and 14 August, respectively. Banding data alone showed similar patterns (Fig. 3, A(B)).

In 1966–1968, the first immatures of both species were identified in the first 10 d of August. Willow Flycatchers built up to an early peak in the period 17–21 August, whereas the peak of immature Alder Flycatchers was in the period 27–31 August (Fig. 1). Despite small sample sizes, these peaks do not appear to result from exceptional conditions in any one year, and moreover, they correspond to double peaks in other banding data for immature Traill's Flycatcher from stations 1 and 2 (Fig. 2).

The median date for estimated totals of immature Willow Flycatchers in 1966–1968 was 23 August (Fig. 3, I(T)), which is 15 d later than for adults. For immature Alder Flycatchers, the median was 28 August, 14 d later than for adults. Thus the medians of the adult and immature Alder Flycatcher migrations were 6 and 5 d later, respectively, than for the same age classes of Willow Flycatchers. The middle 90% of immature Alder Flycatchers occurred in a 30-d period, 11 August–9 September, and Alder Flycatchers in a 26-d period from 17 August–11 September. Banding data alone indicate similar timing (Fig. 3, I(B)).

Four Willow Flycatchers, two Alder Flycatchers and three unidentified birds that were classified as adults by plumage color and wear had small

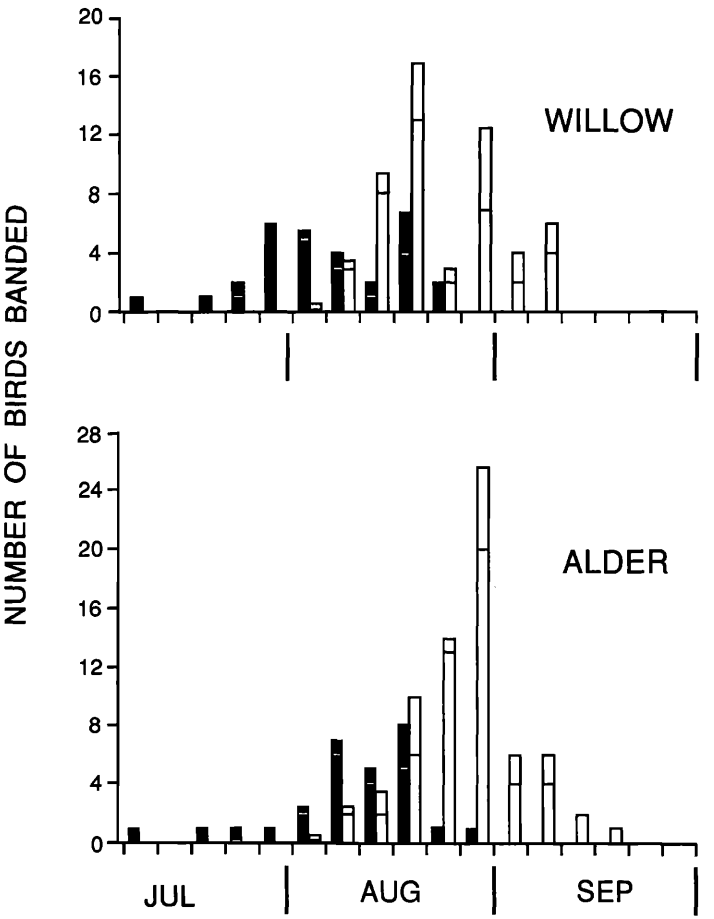

FIGURE 1. Numbers of adult and immature Willow Flycatchers and Alder Flycatchers banded during fall migration at Long Point in successive 5-d periods from 8–12 July through 26–30 September, 1966–1968. Number of birds is combined total for the three years. Solid columns = adults, open columns = immatures. Sections of columns above the horizontal lines represent unidentified birds, each assigned as 0.5 to Willow Flycatcher and 0.5 to Alder Flycatcher (see text).

unpneumatized areas in the skull. These numbers are 17%, 9% and 21% of the samples examined, respectively. One adult Willow Flycatcher that had two unpneumatized areas as large as 8 × 3 mm could have been mistaken for an immature had its plumage not been examined. In all other recorded cases the maximum dimension of unpneumatized areas was no greater than 2 mm.

There was no relationship between wing chord length and date in adult Alder Flycatchers or in either age class of Willow Flycatchers and unidentified flycatchers in fall migration (wing length vs. date, Kendall's

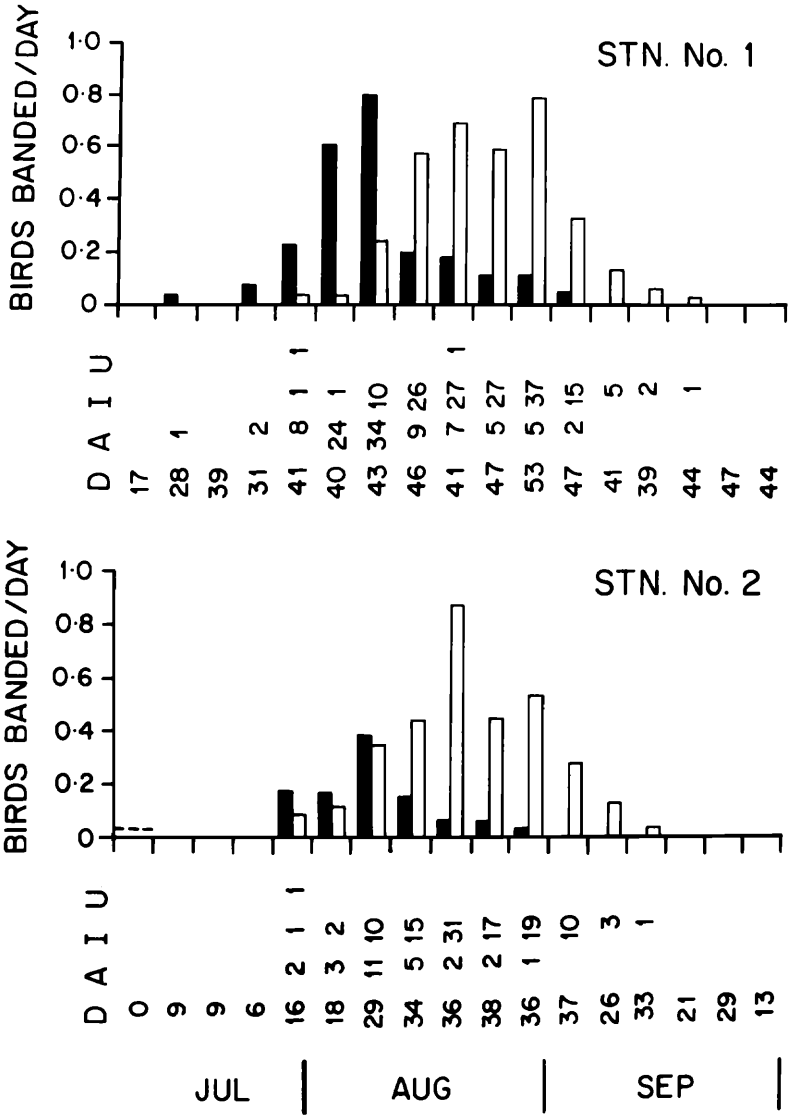

FIGURE 2. Average numbers of adult and immature Traill's Flycatchers banded per day during fall migration at Long Point in successive 5-d periods from 8–12 July through 26–30 September. Upper: station No. 1, 1969–1980. Lower: station No. 2, 1966–1980. Solid columns = adults. Open columns = immatures. Broken horizontal line = no data. D = days of coverage, A = adults banded, I = immatures banded, U = unaged birds banded, for each 5-d period. (Data for days with 50% or more unaged *Empidonax* at any station were excluded. The remaining unaged birds were assigned to age classes in proportion to known age birds before calculating averages for each 5-d period.)

TABLE 1. Numbers of adult and immature Willow and Alder Flycatchers in the fall at Long Point, 1966–1968.

Species	Year(s)	Number of bird-days[a]			Number of banded birds[b]		
		Adult	Immature	% Adult	Adult	Immature	% Adult
Willow	1966	4.3	41.6	9.4	1.5 (0)	15.5 (11)	8.8
	1967	49.6	81.5	37.8	23.0 (18)	28.5 (20)	44.7
	1968	12.7	25.4	33.3	6.5 (6)	12.0 (8)	35.1
	1966–1968	66.6	148.5	31.0	31.0 (24)	56.0 (39)	35.6
Alder	1966	17.0	109.4	13.4	5.5 (4)	33.5 (29)	14.1
	1967	41.6	70.5	37.1	16.0 (11)	27.5 (19)	36.8
	1968	12.3	31.5	28.1	7.5 (7)	10.0 (6)	42.9
	1966–1968	70.9	211.4	25.1	29.0 (22)	71.0 (54)	29.0

[a] Sum of the daily estimated totals over all days.
[b] Unidentified Traill's Flycatchers assigned 0.5 to Willow and 0.5 to Alder Flycatcher. Number of identified birds in parentheses.

τ-b = −0.157–0.129, $P > 0.10$). In immature Alder Flycatchers, there was a significant tendency for short-winged birds to occur earlier than long-winged birds (Kendall's τ-b = 0.169, $P = 0.040$, $n = 54$). This was mainly due to early arrival of short-winged birds: only 1 of 13 immature Alder Flycatchers (8%) trapped before 24 August had a wing chord of 69 mm or more, whereas 25 of 41 (61%) trapped later had wings that long. This may indicate that immature female Alder Flycatchers tend to migrate earlier in fall than immature males, but this conclusion is somewhat suspect, because of the marginal significance level and the fact that six similar significance tests were conducted.

Proportions and total numbers of adults and immatures of both species varied greatly from year to year (Table 1). For the 3 yr combined, adults made up 38.1%, 28.9% and 29.2% of the Willow, Alder and unidentified Traill's Flycatcher bandings, respectively, but these percentages did not differ significantly ($\chi^2 = 1.58$, 2 df, $P > 0.25$).

No adults were molting remiges or rectrices sequentially and symmetrically but a few were replacing tail feathers. Nearly all adults showed some evidence of body molt. Mean body molt scores, ranges and sample sizes for Willow Flycatchers, Alder Flycatchers and unidentified "Traill's" Flycatchers were 0.82 (0–1.6, $n = 24$), 0.60 (0–1.2, $n = 17$) and 1.05 (0.2–2.2, $n = 11$), respectively. Body molt scores of immatures tended to be lower than those of adults: 0.32 (0–1.1, $n = 28$), 0.18 (0–0.9, $n = 27$) and 0.24 (0–1.3, $n = 22$) for Willow, Alder and unidentified flycatchers, respectively.

DISCUSSION

The fall migrations of Alder and Willow Flycatchers at Long Point were similar to each other as well as having features that closely parallel those of the Least and Yellow-bellied Flycatchers (Fig. 4). In this section, all results from Long Point discussed for the latter two species are from

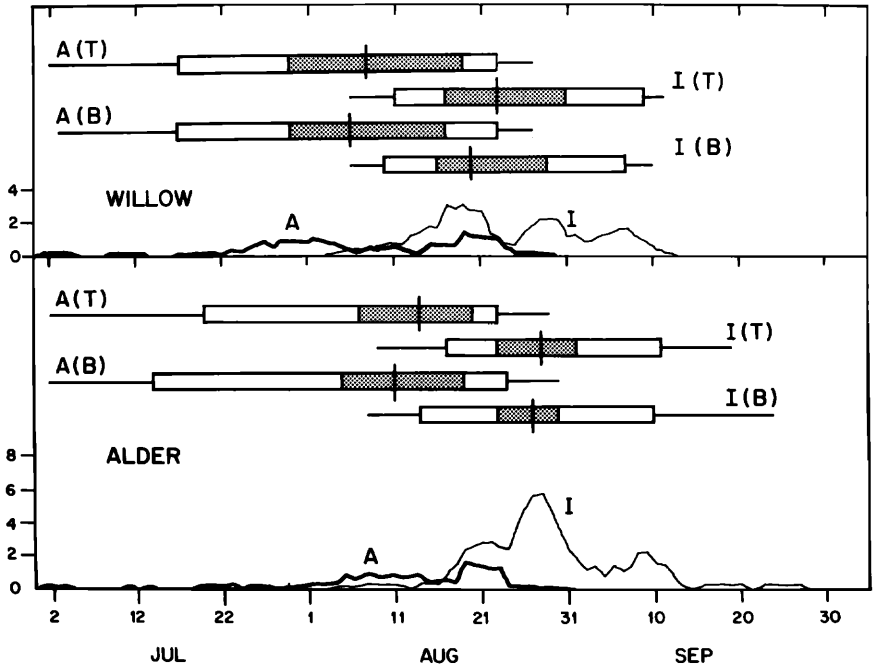

FIGURE 3. Fall migration of Willow and Alder Flycatchers at Long Point, 1966–1968. The continuous lines in the lower sections of each species block show 5-d moving averages of the daily estimated totals for adults and immatures. The bar diagrams in the upper sections show median dates (vertical bars), middle 50% and 90% (stippled and open sections of horizontal bars) and middle 98% (horizontal lines) of daily estimated totals (T) and banded samples (B) for adults and immatures. A = adult, I = immature.

Hussell (1981, 1982b) and for spring migrations of Traill's, Alder and Willow Flycatchers are from Hussell (1991).

In fall 1966–1968, the numbers of adult Alder and Willow Flycatchers were low except in 1967 (Table 1), when adult Least Flycatchers (but not Yellow-bellied Flycatchers) were also exceptionally abundant. Immatures of all four species were relatively numerous in the fall of 1966 and 1967, but not in 1968 (Table 1). The causes of these variations in abundance are not known (Hussell 1991), but it should be noted that my composite analyses of timing of migration (e.g., Fig. 3) are weighted toward years when the respective species and age classes were most abundant.

The proportion of adults among Alder and Willow Flycatchers at station No. 1 in 1966–1968 (25.1% and 31.0% of the estimated totals, respectively, Table 1) was intermediate between those for Yellow-bellied Flycatchers (19.7%) and Least Flycatchers (41.0%). Banding data for other years, however, gave 40.7% adult Traill's Flycatchers at station No. 1 and 23.6% at station No. 2. A lower proportion of adults at station No.

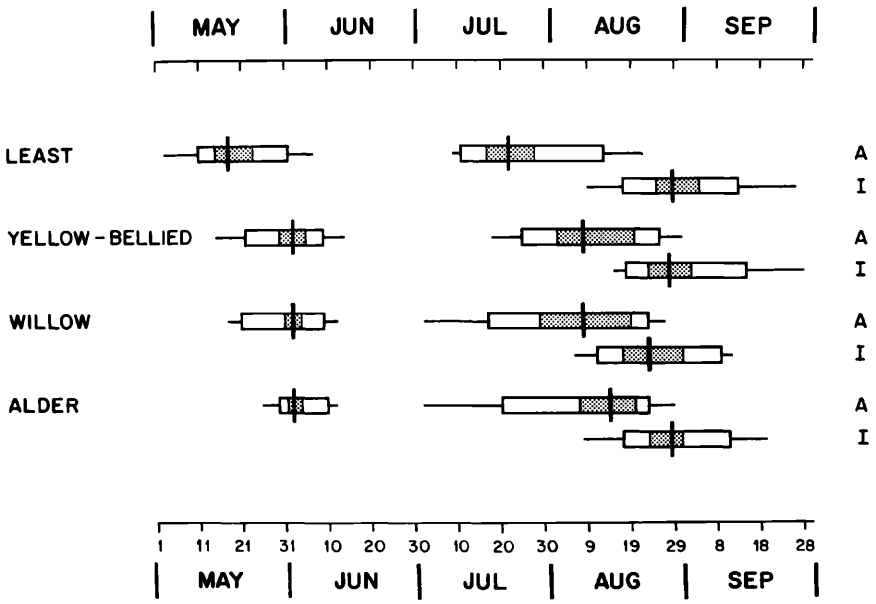

FIGURE 4. Timing of spring and fall migrations of four species of flycatchers at Long Point, Ontario, 1966–1968. Vertical bars, stippled and open sections of horizontal bars, and horizontal lines, represent the median, middle 50%, 90% and 98% respectively, of the daily estimated totals. A = adult, I = immature. Results for Least and Yellow-bellied Flycatchers are from Hussell (1981, 1982b).

2 was also found in Least and Yellow-bellied Flycatchers and is probably site-related, as a similar difference occurs in warblers (Dunn and Nol 1980).

Average numbers of Alder and Willow Flycatchers for the 3 yr combined indicate that adults of the two species were represented in approximately equal numbers at Long Point. Nevertheless, there was an overall preponderance of immature Alders in fall (Fig. 3, Table 1) in contrast to greater numbers of Willows in spring. Both Yellow-bellied and Least Flycatchers were more abundant than Willow or Alder Flycatchers, with Least Flycatchers by far the commonest of the four species.

Nearly all adults and immatures were molting body plumage in the fall but there was no sign of flight feather molt. Fall molt scores of Alder and Willow Flycatchers were similar to those of Yellow-bellied Flycatchers and substantially lower than those of Least Flycatchers. Body molt also occurred in most Least Flycatchers in fall migration in Manitoba (Sealy and Biermann 1983).

Fragmentary data from Kansas on the fall migration of Traill's Flycatchers are in agreement with the Ontario observations. Twenty records occurred from 23 July to 12 September with five of seven adults by 16 August, the first date on which an immature was taken (Ely 1970). No

detailed information has been published previously on the timing of fall migrations of Alder or Willow Flycatchers. On Long Island, New York, in 1961–1965, fall migration of Traill's Flycatchers extended from 11 August to 18 September with only 10 of 92 birds aged as adults (Phillips et al. 1966). Those dates agree with the timing of migration of immatures at Long Point. Of 80 individuals tentatively identified by Stein's (1963) formula, only three were Willow Flycatchers and the remaining 77 were Alders. This distribution was in accordance with expectations, in view of the preponderance of breeding Alder Flycatchers in New England and northeastern Canada. Nevertheless, some Willow Flycatchers may have been misidentified as Alders by Phillips et al. (1966) because they did not recognize that immatures have shorter bills than adults (Hussell 1990).

Median dates of fall migration of adult Willow and Alder Flycatchers were 67 and 73 d after spring medians, respectively (Fig. 4). Assuming a 1-night flight to and from Long Point, adult Willow and Alder Flycatchers were on the breeding grounds for an average of no more than 66 and 72 d, respectively. This compares with an estimated 64 and 66 d for Least and Yellow-bellied Flycatchers, respectively (Hussell 1981, 1982b). The far northern distribution of the Alder Flycatcher suggests that a 1-d flight may be an underestimate and 72 d on the breeding grounds an overestimate. The sequence of fall migration of adults of the four species was similar to that in spring. Leasts were earliest with a median date on 22 July followed an average of about 17 d later by Yellow-bellied and Willow Flycatchers. Adult Alder Flycatchers overlapped broadly with those of the latter two species, but most tended to migrate later with the median an additional 6 d later on 14 August. In all four species, southward migration of adults occurred before the post-nuptial molt of the flight feathers. Thus the short period spent on the breeding grounds and early fall departure of adults following breeding is very similar in these four species and is undoubtedly related to the timing of the post-nuptial molt of the flight feathers, which occurs on the wintering grounds (Dwight 1900; Hussell 1980, 1982a; Johnson 1963).

Immatures of all four species migrated later than adults. Despite differences in timing of migrations of adults, immature Least, Yellow-bellied and Alder Flycatchers migrated almost simultaneously with medians on 29, 28, and 28 August, respectively. This resulted in an adult-immature difference in timing of 38 d in the Least, 20 d in the Yellow-bellied and only 14 d in the Alder Flycatcher. Immature Willow Flycatchers migrated 5–6 d earlier than immatures of the other three species (median = 23 August), which gave an adult-immature difference in medians of 15 d, about the same as for the Alder Flycatcher (14 d).

Sealy and Biermann (1983) speculated that early departure of adult Least Flycatchers prior to collapse of the food supply, may be due to competition for winter territories. They suggested that immatures are unlikely to be able to establish territories in Central America, and therefore there is probably no advantage to them in migrating early. The almost identical timing of fall migration of immatures of the four species

of *Empidonax* at Long Point, strongly suggests that their migrations are timed to avoid a decline in the supply of aerial insects on the breeding grounds.

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