NOTES ON THE LIFE HISTORY OF TRAILL'S FLYCATCHER (*EMPIDONAX TRAILLII*) IN SOUTHEASTERN WASHINGTON

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THE recent growth of interest in the nesting ecology, voice, and habits of Traill's Flycatcher (*Empidonax traillii*) in relation to the taxonomic segregation of this species into its several races prompts me to record these observations on the hitherto neglected western race, *E. t. brewsteri*. Recurrent disagreements and difficulties regarding racial differentiation, particularly in the West (*cf.* Aldrich, 1951; Phillips, 1948; Miller, 1941), render field studies of Traill's Flycatcher in various parts of its range an especially pertinent adjunct of taxonomic studies based on museum skins, as Berger and Parmelee (1952) have previously stated. Although the present study is not aimed at a principally taxonomic target, items of potential taxonomic significance, such as voice and nesting habitat, have been given special emphasis and are compared with similar phenomena elsewhere in the range of the species. The population of *Empidonax traillii* discussed below lies within the range of the proposed race *adastus* (Oberholser, 1932; Aldrich, *in litt.*), but the older racial name must be retained in this paper, pending acceptance of *adastus* by the American Ornithologists' Union's Committee on Classification and Nomenclature of North American Birds.

The area concerned in this study is a tract of approximately two hundred square miles lying north and northwest of Pullman, Whitman County, southeastern Washington. During the spring and summer of 1952, I was afield during 121 days and engaged in a general survey of the breeding bird population by intensive studies at 5 major and 11 minor stations and by extensive periodic reconnaissance trips throughout the tract. Although this study was not devoted to any particular group or species, it yielded a thorough qualitative appraisal of the habitat distribution of Traill's Flycatcher and much preliminary data concerning its behavior and nesting ecology. I examined 22 nests in 1952, but it was not possible to revisit them regularly, and only partial histories were obtained. During 1953, I was able to spend only late afternoon hours and an occasional weekend in the field between 15 May and 30 August. Most of this time was utilized in the intensive study of a restricted population of Traill's Flycatchers four miles north of Pullman, although some time was also spent in observation and nest-searching throughout the area studied the previous year. Information on the growth of nestlings, population

density, and further data concerning nesting ecology and the voice and behavior of the adults were obtained. Twenty nests were examined during this year, and essentially complete histories were obtained for many of them.

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Physiography of the study area.—The general topography of the study area is one of mature, dune-like hills which originated in early Pleistocene time as windborne deposits of dust stripped from the arid lands to the west and southwest (Treasher, 1926). These are the so-called Palouse Hills of southeastern Washington and adjacent Idaho, lying at middle altitudes between the forested Bitterroot Range and the arid semi-desert of central Washington. The general altitude of the study area is about 2500 feet, and a series of "buttes" which extend into it from the nearby mountains of Idaho rise abruptly above the rolling hills to heights of 3650 feet. A dendritic pattern of streamlets dissects the uplands, but only the north and south forks of the Palouse River, bounding the study area on three sides, and one or two of their larger tributary creeks, maintain a permanent flow. Because of the porous nature of the soil and the great depth to bedrock there are no natural lentic bodies of water in the area. Springs and percolation sinks which might support marsh vegetation are uncommon and frequently are dry by midsummer.

The aboriginal vegetation of this portion of the Palouse Hills was a climax of prairie grasses dominated by *Festuca idahoensis* and *Agropyron spicatum*, with interspersed communities of brush species (Daubenmire, 1942). During the past fifty years most of the prairie vegetation has succumbed to the plow, and it is only in gullies or on north slopes too steep to cultivate that remnants of the prairie persist as "islands" in the sea of wheat. These dry upland remnants are often dominated by their shrubby elements, such as hawthorn (= western black haw, *Crataegus douglasii*), chokecherry (*Prunus virginiana* var. *melanocarpa*), snowberry (*Symphoricarpos rivularis*),

and roses (*Rosa* spp.). Along creeks and streamlet valleys, hawthorns, frequently assuming the stature of small trees, form extensive thickets, and there is an undergrowth and edge growth of shrubby willows (*Salix* spp.), rose, reed canary grass (*Phalaris arundinacea*), and many rank forbs, among which cow parsnip (*Heracleum lanatum*) is the most conspicuous. In certain stream valleys the dominant hawthorn trees are separated by areas of low meadow grasses and forbs, giving an open, park-like aspect. Locally, on the narrow flood-plain of the Palouse River, stands of black cottonwood (*Populus trichocarpa*), quaking aspen (*Populus tremuloides*), mountain alder (*Alnus tenuifolia*), and caudate willow (*Salix caudata*) may form rather dense groves, with a shrub stratum, often, of lesser willows, chokecherry, hawthorn, and other species. Coniferous vegetation invades the area from the east via the north exposures of the aforementioned "buttes" and the relatively deep North Palouse River Canyon. Ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga taxifolia*) are the dominants of two rather distinct zones which occur in a mosaic in these situations. Extensive chaparral-like thickets of ninebark (*Physocarpus malvaceus*) occur as open stands in clearings and along the forest edge. A well-defined stratum of shrub species is present in the pine woodland but is scant or absent in the more dense Douglas fir forest.

The climate of the Palouse Hills is characterized by wet, cool winters and warm, dry summers. About seventy per cent of the annual rainfall, which averages approximately twenty inches, occurs between mid-October and late March. July temperatures average 62° F., and midsummer highs of 104° F. have been recorded at Pullman (Fisher, 1941). The weather during 1952 and 1953 will be discussed in conjunction with the nesting season during those years.

The pre-nesting season.—The main wave of spring migrants of *Empidonax traillii* arrives at Pullman in late May or early June. My earliest records for more than single birds in 1952 and 1953 were, respectively, 29 May and 8 June. The fourteen-year study by Hudson and Yocom (1954) reports an early date of 28 May for southeastern Washington in general. Shaw's (*in* Jewett *et al.*, 1953) date of 10 May 1920 for Pullman is an exceptionally early one. The infiltration of the nesting habitat was rapid in 1952, and it would appear that essentially the entire nesting population arrived in the area within a period of six or seven days. Pairs and trios engaged in vigorous sexual chase, and others, apparently already mated, were observed as early as 1 June during that year, making it plain that males and females arrived here almost simultaneously.

Territorial disputes among males are frequent and violent during the pre-nesting period, and occasionally an invading male is attacked by both members of a territorial pair. Rarely this attack involves physical contact, but typically consists, after preliminary vocalizations, of a swift and intricate pursuit flight and much additional calling on the part of both defender and invader. Participation by females in pursuit flight, in three recorded instances, did not go beyond a single swoop at the invader. These birds were identified as females by their silence and by their close association with the defending males.

By the time the laying season began there was rarely any territorial fighting in populations which I observed (although the querulous twittering of the intimidation call could occasionally be heard), and territorial boundaries seemed to be well adjusted. The reputed pugnacity of Traill's Flycatcher toward birds of other species (*vide* Wheelock, Bendire, *in* Bent, 1942: 202; Dawson and Bowles, 1909: 389) is either much over-rated or does not apply to the species in this area. I have recorded only one instance of such behavior, the harassing of an Eastern Kingbird (*Tyrannus tyrannus*).

Habitat.—As with populations of *Empidonax traillii* in the East and Midwest (Snyder, 1953; Berger and Parmelee, 1952; Meanley, 1952; Campbell, 1936), this species nests in xeric uplands as well as relatively mesic riparian sites in the Palouse Hills. However, this is apparently not the case throughout the West, and certain authors report the species only from moist, brushy habitats. Grinnell and Miller (1944: 257) in California found *E. t. brewsteri* "strikingly restricted to thickets of willows, whether along streams in broad valleys, in canyon bottoms, around mountain-side seepages, or at the margins of ponds and lakes." Sumner and Dixon (1953: 123) offer an almost identical analysis for the Sierra Nevada, and Dawson (1923: 885) also emphasizes an affinity for willows in California, adding that Traill's Flycatcher is "a lover of the half-open situations, brushy rather than timbered, of clearings, low thickets, and river-banks." Hand (1941: 227), in northern Idaho, found the species limited during the breeding season to "willow-bordered mountain streams or brushy deciduous growth in the larger valleys." Behle (1943:46) reports a similar habitat preference in southwestern Utah. For Oregon, Gabrielson and Jewett (1940: 395) mention only "wooded stream bottoms."

In Washington in particular, Rathbun (*in* Bent, 1942: 198) analyzes the habitat of *E. t. brewsteri* west of the Cascade Range as "quite open places more or less overgrown with shrubs or bracken or both, the

location of which is along the margin of a mixed growth of trees, mostly deciduous, with water or low ground not far away." In southeastern Washington, Traill's Flycatcher is not confined to streamside brush or even to moist sites, and as Wing's (1949) census emphasizes, may be found also in dry, brushy prairie remnants in the uplands. Dawson and Bowles (1909: 389) mention in passing an apparently similar dry-land occurrence in western Washington. Dumas' (1950) extensive analysis of breeding bird distribution in two counties south of the Snake River in Washington reports Traill's Flycatcher in substantially the same range of vegetation types in which I have found the species in the present study area. This habitat may be divided, on the basis of floristic differences, into four general segments: (1) riparian hawthorn thicket, (2) the shrub stratum of the less dense portions of flood-plain forest, (3) upland prairie remnants containing hawthorn, chokecherry, or rose, and (4) dry ninebark thickets at the lower edge of the coniferous forest zone.

In an area such as the Palouse Hills, where Traill's Flycatcher is found in nearly all vegetation types containing a shrub stratum (for exception see below) and where the ecological edge effect (Leopold, 1936: 131) is emphasized by the small size or irregular configuration of brushy habitats, it is practically impossible to discover, through observation of the presence or absence of the bird, even the major factors determining its habitat selection. This is unfortunate, since the phenomenon of habitat selection is manifestly an inherent behavior pattern (Beecher, 1942), and an analysis of the factors involved could conceivably shed much light on the suspected ecological segregation of the various races of *E. traillii*. Although the vegetation types selected by Traill's Flycatcher in the Palouse Hills have certain features in common, from the human conception of the demands that the nesting economy makes upon the vegetation, there is no rigorous method of determining the importance of these factors to the bird itself. However, for purposes of comparison with populations of *E. traillii* in other areas, the more salient ones will be briefly noted.

The shrub lands occupied by Traill's Flycatcher are in general quite open, with the bushes well spaced in the subordinate herbaceous vegetation. The few remaining dense, extensive thickets are typically bordered by open fields, and it is on this edge that Traill's Flycatcher is found. In the flood-plain forest, the bird likewise avoids the dense alder and willow thickets and is found on the higher benches where the shrubs are more widely spaced and less shaded. The species does not penetrate deeply into the coniferous forest zone but is found only along its lower edge or where a lobe of prairie vegetation or ninebark thicket extends into it.

Nesting substrate.—The concept of nesting substrate as an important limiting factor in habitat distribution has been thoroughly discussed by Beecher (1942). Detailed remarks concerning nest-site selection appear below, and it is sufficient here to point out that a suitable habitat must provide low crotches or forks of branches sufficiently small that the sides of the nest may be woven to them. Suitable sites of this type are found in all of the brushy draws and slopes of the Palouse Hills, and Traill's Flycatcher occurs in all of them except the understory of the coniferous woods. It is interesting to note that here the niche is occupied by Wright's Flycatcher (*Empidonax oberholseri*), whose habits are very similar to those of Traill's Flycatcher. These two species may be found nesting almost side by side at the lower edge of the pine woods on the slopes of certain of the "buttes" in the study area and also along the pine woods occupying the canyon slopes of the North Palouse River, but in the interior of the forest and higher on the slopes Traill's Flycatcher is absent.

Song perches.—Many miles of rose-snowberry thicket fringe rural roads and fencelines in the uplands, but Traill's Flycatcher, in my experience, does not occur in this vegetation type except where a hawthorn or chokecherry bush rises above the lower thicket, or where a low-hanging telephone line occurs. I believe that its occurrence in rose-snowberry thickets is dependent upon the presence of an elevated, exposed song perch. In view of the conspicuous role of song and song periodicity in the sexual cycle of this species, it would be very reasonable to assume that a strong perch predilection accompanies singing behavior. Lack (1933: 247) has demonstrated a similar habitat requirement in the Tree Pipit (*Anthus trivialis*) in England. Low perches, such as fence wires, are not consistently utilized as territorial song posts, and I have never observed them used as perches during the twilight song period. In general, the principal song perches are the highest exposed twigs in the territory, and they vary from about seven or eight feet above the ground in the lower shrubbery of the uplands to as high as 28 feet in the arborescent hawthorns of the riparian thickets. It is quite common during the early part of the evening song period to drive along the edge of a thicket and see Traill's Flycatchers silhouetted against the pale background of wheatfields, each bird perched on a high, bare twig.

Shade, cover, and water for drinking seem to have little or no influence on the distribution of Traill's Flycatcher in this area. Some territories, such as those in openings of the hawthorn thicket, include a dim, shaded retreat beneath the closed tree crown; others are barren of shade for either adults or for the nest, with the exception of whatever shade is afforded by a few overlapping leaves. Although the species

is rather retiring, it is not skulking or furtive. Dense refuge cover is not required, and a thin screen of rose leaves may serve as well as any other type. The availability of surface water is likewise not a requirement, at least not after the early part of the nesting season. The average estimated distance of 40 nests from surface water was 123 feet, between the extremes of 3 feet and 600 feet. In many cases water sources were dry before the nesting cycle was complete, and often before the eggs had hatched. Dew-fall in the Palouse Hills during the summer months is extremely rare.

Nest site.—Traill's Flycatcher chooses a nest site providing a vertical crotch, or a horizontal or slanting fork providing support from below. This latter feature is apparently essential, since the first stage of nest-building consists of placing a wad of soft strips of vegetation in a crotch as a platform for further construction. In addition, the nest site must provide twigs of small diameter (⅛″ to ¼″) to which the nest may be woven. Cover is not an essential factor, for nests are as frequently found in exposed sites as in well-hidden ones. Traill's Flycatcher in this area seems to have a very definite nest-height preference, 34 of 41 nests (83 per cent) were between 20 inches and 40 inches above the ground. This preference is especially noticeable because nesting crotches apparently identical to those used are available at much greater heights. The height of nests above the ground, the substrate species, and crotch type are given in table 1.

TABLE 1

NEST SITES OF TRAILL'S FLYCATCHER IN WHITMAN COUNTY, WASHINGTON

Substrate	*Number of Nests*	*Height above Ground*		*Crotch Type*	
		Average	*Extremes*	*Horizontal*	*Vertical*
Rose (*Rosa*)	15	35″	24–61″	1	14
Hawthorn (*Crataegus*)	8	32	16–53	6	2
Cow parsnip (*Heracleum*)	7	27	16–36	—	7
Choke cherry (*Prunus*)	5	32	20–42	—	5
Ninebark (*Physocarpus*)	3	36	34–38	1	2
Willow (*Salix*)	1	—	66″	—	1
Cottonwood (*Populus*)	1	—	28	—	1
Groundsel (*Senecio*)	1	—	26	—	1
Apple (*Malus*)	1	—	61	—	1
Totals and Averages	42	32.4	16–66	8	34

Berger and Hofslund (1950: 9) give 49.5 inches as the average height above the ground of 17 *Empidonax traillii* nests in Michigan, with extremes at 41 inches and 63 inches. Other nesting heights were estimated up to ten feet. Meanley (1952) reports the average height of 15 nests (13 of which were in *Crataegus*) as 7.5 feet in Arkan-

sas. Howsley's records (*in* Bent, 1942: 199) from western Washington give an average nest height of three feet, between the extremes of 30 inches and 5.5 feet. Other western nests have been found as high as 18 feet (Bent, 1942: 200).

In shrubs, the nest is almost invariably placed in the peripheral foliage, and in thickets it will typically be found in the outer edge, a situation also noted by Berger and Parmelee (1952: 37) in Michigan. This choice may in part be dictated by the habit of the female of approaching the nest in a single swoop, when she is unaware of the observer, without any preliminary skulking. This habit has also been recorded by Farley (1901: 355) for *Empidonax traillii* in eastern Massachusetts.

Structure of the nest.—Two general nest types may be described for Traill's Flycatcher is the Palouse Hills: a deep, relatively thick-walled structure usually found in vertical crotches, and a flat, relatively thin-walled type usually found in horizontal or slanting forks. In reality, these "types" are the extremes of a series, form being dependent upon the mechanical support afforded by the substrate, and many intermediate nests have been observed which are "typical" of neither those in vertical nor in horizontal supports. There is a definite tendency, however, toward more bulky nests in vertical crotches, and less bulky nests in horizontal forks. Much comment has been given in the literature regarding the apparent geographical segregation of two nest types referred to as "Yellow Warbler-like" and "Song Sparrow-like" (*vide* Aldrich, 1953; Snyder, 1953). The two extreme "types" which occur in this area superficially resemble, on the one hand, the compact nest of the Yellow Warbler (*Dendroica petechia*), and, on the other hand, the more bulky and ragged nest of the Song Sparrow (*Melospiza melodia*). There is no correlation between these nest types and the habitat in which they are found or behavior of the Traill's Flycatchers which constructed them. I can only conclude that they are normal structural variants within the population of *Empidonax traillii* here discussed.

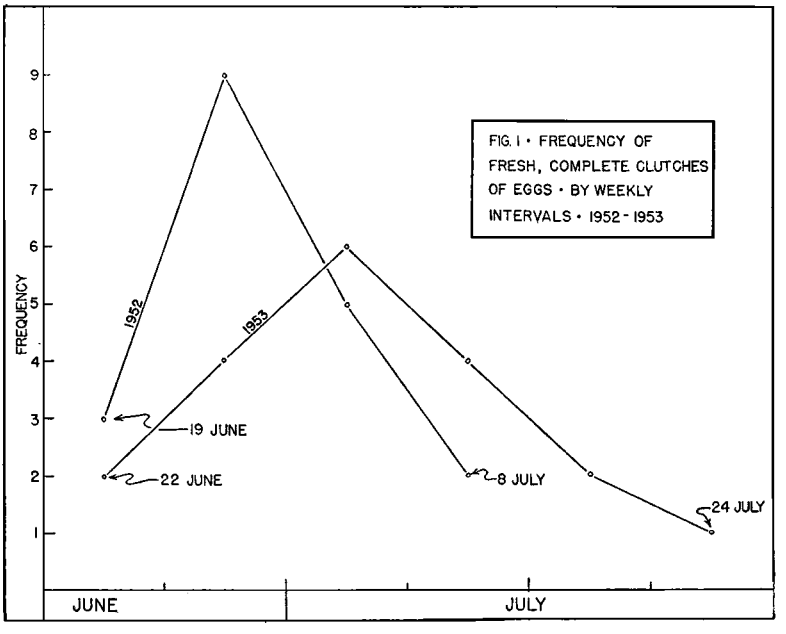
The structure of the nest is best described with reference to the building program. Although I have not been able to observe the construction of any nest from start to finish, I have examined nests in many phases of construction. When placed in sequence, these observations agree closely with those of Howsley (*in* Bent, 1942: 199) with regard to the building program: *Stage 1:* the piling of soft bark strips, dried grass leaves, or plant floss in the selected nesting site. In a vertical crotch, this material is simply laid at the point of divergence of the component stems; in a horizontal or slanting fork the material is placed usually upon a complex of underlying interwoven stems of the nest bush. It serves simply as a foundation or filling, and its mass is dependent apparently upon the distance from the supporting twigs

to the point where the nest structure may be woven to the selected fork. In vertical crotches the mass of the foundation material is seemingly a function of the angle of divergence of the component twigs of the crotch. The narrower this angle is, the greater the distance from its base to a point where its diameter will accommodate the rim of the finished nest. Much loose foundation material is required in such a site, and this fact no doubt accounts for the typically ragged and bulky nests in vertical crotches. Occasionally the foundation material is bound with a few strands of animal silk. *Stage 2:* When the foundation material is sufficiently deep, a cradle is next woven upon it. Loose ends of foundation material are incorporated in this cradle which joins the twigs of the nest site and serves both to anchor the nest and as a receptacle for additional nest material. Soft, pliable strips of plant tissue are used in its construction. *Stage 3:* Additional loose material is next placed in the cradle until there is a sufficient mass to support the cup of the nest. *Stage 4:* The rim and cup of the nest, unlike the major bulk, are sturdily and rather neatly constructed. Upon the secondary foundation material in the cradle, stiff, dry grass stems are laid and turned to form a tight rim. Infrequently, a binding of animal silk or strands of *Populus* floss may be added. The bird applies this material using the mandible like a trowel, at the same time squatting in the cup of the nest and turning around and around, shaping the cup to its body. The lining of the cup is woven from wiry rootlets or stiff grass stems, and often from both. An inner layer of horsehair was found in two nests. Materials which contribute nothing to structural integrity, such as wads of plant floss, or one or two feathers, are occasionally included in the rim or outer bulk. These are not present in conspicuous proportions. Two features of the nest of Traill's Flycatcher are very frequently observed, and almost constitute "key" characteristics. These are the tangential protrusion of the ends of the long grass stems used in the construction of the rim of the nest, and the occurrence of one or two long grass stems dangling from the major bulk of the nest.

The average and extreme dimensions of 20 nests (five from horizontal forks, 15 from vertical crotches) from the Palouse Hills are, in inches: *cup diameter,* 2.1 (2.0–2.2); *cup depth,* 1.5 (1.4–2.0); *outer (maximum) diameter,* 3.4 (3.0–4.0); *outer depth,* 3.3 (2.2–4.9). Stevenson (1942:68), for an unspecified number of Pacific States nests, gives these dimensions, in the same order, as: 2.1, 1.4, 3.7, 2.3. Berger and Hofslund (1950:8) report these dimensions for 28 *Empidonax traillii* nests in Michigan as: 2.15 (1.75–2.25), 1.38 (1.00–2.00), 2.54 (2.13–3.00), 2.53 (1.88–5.00). As might be anticipated, the dimensions of the cup vary within narrower limits than do the overall dimensions.

Population density.—Wing (1949) found an average of 9.2 breeding pairs of Traill's Flycatchers per hundred acres of Palouse prairie during a five-year study. My 1953 study plot on Missouri Flat Creek, four miles north of Pullman, contained 12 nests (10 found plus two estimated) on 86.5 acres, or 14 breeding pairs per one hundred acres. This census area is a rather narrow strip of alternately dense and open hawthorn thicket along a running stream. Other major vegetation of the plot consists of thick stands of cow parsnip, particularly in clearings and along the edge of the more dense thicket, fence-rows of dense rose shrubbery, and a few bushy willows along the stream bank. The thicket is sharply delimited on the south by open wheat and pea fields and bordered on the north by a railroad,

county road, and more open fields. The foraging areas of the flycatchers extended only a few yards into the wheatfields on the south, and rarely further than the road on the north. In measuring the area of the sample, by plane table and planimeter, these facts were utilized in fixing its boundaries.



Traill's Flycatchers are locally rather common in the flood-plain forest but are uncommon in ninebark chaparral. Although I have no quantitative data regarding these latter two divisions of the habitat, my opinion is that the species is less abundant in either of them than in the riparian hawthorn thickets which apparently form the optimum habitat for Traill's Flycatcher in the Palouse Hills.

Chronology of the nesting seasons, 1952 and 1953.—Figure 1 compares the 1952 and 1953 nesting seasons in terms of the incidence of fresh, complete clutches of eggs. Each curve is based upon 19 clutches. For a majority of the 1952 nests, and some of the 1953 nests, these dates for the complete, fresh clutches were obtained by a process of extrapolation based on the known or closely estimated age of the nest contents at some stage of their development. This method has previously been utilized by Lack (1950), Beecher (1942), and others in a similar manner. Errors inherent in the method arise from individual variation in the incubation and nestling spans and

from the fact that some birds apparently begin incubation following the laying of the second egg. Hence, some clutches designated as "fresh" may have had two eggs which had been, on the average, incubated for 24 hours. Taking into account all known sources of variation, the least reliable of my data are subject to a possible error of ± 3.5 days. Sixteen per cent of the 38 dates are thus affected, the remainder being subject to lesser possible errors down to a few hours. Statistically, one may expect these errors to tend to cancel one another except at the limits of the curves. Fortunately, the dates of earliest known incubation in both years have possible errors no greater than ± 12 hours. The incubation period in these calculations is taken to be 12 days (Burns, 1915; Bendire, 1895), and the nestling period to vary from 13 to 15 days (Burns, 1921; Berger and Hofslund, 1950).

Three major features are evident in comparing the chronologies of the nesting seasons of 1952 and 1953: (1) The close coincidence of the dates of earliest known incubation, (2) the protracted (by about 16 days) 1953 season, and (3) the lower and later (by about one week) peak of activity in 1953. The total span of the nesting season in 1952, considered as the interval between the laying of the earliest known egg and the fledging of the latest known young, was 46 days. In 1953 this span was 67 days.

Nesting chronology in relation to phenology.—It would be absurd to attempt to determine on the basis of the meager data available even the major environmental factors influencing the nesting periodicity of Traill's Flycatcher. However, certain observations regarding the possible relation of weather and of seasonal progress as reflected by plant phenology are suggestive; these are noted here for the consideration of other students of *Empidonax traillii*. A comparison of the weather in 1952 and 1953 is shown in Table 2. March of 1953 was warmer than that month of 1952, but the rest of the spring and early summer was considerably colder than in 1952. Vegetative growth, which in the principal species began prior to the temperature

TABLE 2

COMPARATIVE WEATHER DATA, 1952–1953 (U.S.D.C., 1953)

	Precipitation		*Mean Temperature*	
	1952	*1953*	*1952*	*1953*
March	1.15″	1.74″	37.2 F.	40.4 F.
April	0.94	1.37	50.3	45.7
May	1.21	1.13	55.5	51.5
June	2.94	1.09	59.4	55.5
July	0.07	0.00	68.2	66.6

recession, followed similar patterns during the two years, and by mid-June vegetation density in Traill's Flycatcher habitat was apparently identical. Many of the May and June dates of first bloom, however, were much retarded in 1953 and reflected a general biological "lateness" of that year as compared with the preceding one (phenological dates were obtained by the method of the extensive survey, following principles established by Leopold and Jones [1947]). Seven shrubs and forbs for which I have extensive data for the two years bloomed later in 1953 by an average of 13 days; *i. e.*, *Rosa* spp., 14 days; *Crataegus douglasii*, 7 days; *Prunus virginiana* var. *melanocarpa*, 12 days; *Physocarpus malvaceus*, 15 days; *Lupinus sericeus*, 13 days; *Camassia quamash*, 8 days; *Iris missouriensis*, 15 days. This "lateness" was obviously shared at least in part by Traill's Flycatcher, as manifested by the later and lower peak of nesting activity and the protraction of the nesting span. In my opinion, this tardiness was not the result of any mechanical deficiency in nesting sites, as McCabe (*in* Leopold and Jones 1947: 108) has very reasonably suggested for *Empidonax traillii* in Wisconsin. The shape of the curve for 1953, in comparison with that of 1952, suggests a relatively large percentage of first-nest failures, but my data offer nothing to confirm this hypothesis. It is possible, also, that the considerably later blooming dates in 1953 had a significant quantitative effect on the periodicity of insects used as food for the nestlings of this species, as McCabe has previously postulated for Traill's Flycatcher in Wisconsin. Lack (1950) emphasizes the food supply for nestlings as a major "ultimate factor" (*i.e.*, one operating through natural selection to bring about a coincidence of breeding season and food supply for the young) modifying the breeding periodicity of birds of the North Temperate Zone in Europe.

Within the framework of seasonal retardation which has been discussed above, one factor stands out as anomalous; *viz.*, the close agreement of dates of earliest eggs in 1952 and 1953. This is all the more conspicuous because of the comparatively large average temperature differences occurring during the first fifteen days of June in those two years (59.6° F. in 1952, 55.0° F. in 1953), and because of the very heavy rainfall (230 per cent of average) during June of 1952, as compared with subnormal precipitation (82 per cent of average) in 1953. A detailed analysis of daily average, minimum, and maximum temperatures failed to reveal any pattern with which this temporal coincidence could be correlated. It is entirely possible that it is, in fact, a coincidence; but it would be inadvisable to ignore the possibility that it may also be a response principally to some

annually recurring change in environment, such as increasing photoperiod.

A possible phenological indicator.—Certain species of plants, as Leopold and Jones (1947: 113) point out, are governed principally by photoperiod in their annual growth cycles and show only small year-to-year differences in phenology. Such species in our area appear to be yarrow (*Achillea lanulosa*), with a date of earliest bloom two days later in 1953 than in 1952, and cow parsnip (*Heracleum lanatum*), which first bloomed three days later in 1953 than in the preceding year. This latter species is a conspicuous element in the streamside habitat of Traill's Flycatcher in the Palouse Hills, and an apparent correlation occurs between dates of its first bloom and of first eggs of the flycatcher. Both of these phenomena were three days later in 1953 than in 1952, with a lapse of 20 days between first observed bloom and first known egg. *Heracleum* has a continent-wide distribution, and comparative data from other areas would be very interesting.

Incubation period.—Little has been recorded on the incubation period of *Empidonax traillii*. Burns (1915), probably citing Bendire (1895), gives 12 days. Dawson and Bowles (1909: 389), perhaps using the same source, concur. Although individual variation among clutches and variations arising from environmental differences undoubtedly modify this datum, 12 days probably represent an average incubation period. Several clutches which I had marked for incubation studies were all lost to predators before hatching, and data obtained incidentally from other nests, although tending to confirm a 12-day period, do not improve what is already estimated.

Growth of nestlings.—Studies of four broods, one of them containing a nestling Brown-headed Cowbird (*Molothrus ater*), were begun in 1953. Only one of these broods was successfully fledged. Inasmuch as the parasitized brood was excluded in summarizing the growth data, the information presented below is based upon nine nestlings for the first three days of nestling life and for lesser numbers thereafter. (See table 3 and figure 2.) All weights were taken on a single-beam, agate-bearing balance accurate to 0.1 gm. Feather lengths were measured with a millimeter rule, interpolating to the nearest 0.2 mm. It was possible to visit each nest only once daily, for measuring purposes, between 6 P.M. and 7:30 P.M. The time of daily visits to individual nests varied within less than one-half hour. At no time, even late in nestling life, was any difficulty encountered with weighed birds not remaining on the nest when replaced there. This is in accord with the observation of Lack and Silva (1949: 64) that regular visits, begun at an early age, to broods of English Robins (*Erithacus*

rubecula) eliminated the escape reactions found in young of this species when first encountered at a later stage of nest life. In common with this species, *E. t. brewsteri*, if older than about seven days of age when first encountered, readily flees the nest.

An effort was made to visit the nests at least twice daily during the anticipated hatching period, but this was not always possible. When eggs were found in a nest on one day and nestlings on the following day, this latter day was designated as "day 0.5" of nestling life, after the method of Lack and Silva (1949), since, on the average, nestlings would be twelve hours old when found. Based on six estimated hatching times, my birds averaged about ten hours old when first examined. Days subsequent to the hatching date are designated 1.5, 2.5, and so on. As Lack and Silva (1949) note, this method is more accurate than denoting the first day as "day 0" or "day 1" and avoids the confusion inherent in these alternative notations.

The newly hatched nestling.—Weights of nestlings with some portion of the dorsal down still moist after hatching were 1.4, 1.4, 1.6, 1.0, and 0.9 gm. The last two weights are from a nest containing a nestling cowbird and are no doubt atypical. At this early age, and until about day 2.5, the nestling assumes an embryonic posture in the nest, resting on the huge abdomen and the crown of the turned-under head. At first, there is no gaping response to jiggling of the nest, but this appears within twelve hours after hatching. Copious, long Mouse Gray down (all capitalized color names after Ridgway, 1912) clothes the crown, and tufts of shorter down, Pallid Neutral Gray in color, occupy the spinal and alar tracts. The positions of the humeral, femoral, and crural tracts are indicated by three or four down feathers each, and about seven down feathers are present on each side in the abdominal portion of the ventral tract. The remigial papillae are visible through the skin of the wings as minute blue-black dots. Coloration of soft parts is as follows: *gape*, Cadmium Yellow, remaining this color throughout nestling life; *rictus*, Pinard Yellow, darkening slightly later; *rhamphotheca* and *podotheca* Orange-buff. By day 6.5 the thecae have altered to Ochraceous-buff and Apricot Yellow in blotches. At about twelve days, the *gonys* is near Flesh-color, the *culmen* Vinaceous Fawn, and the *tarsus* various tones near Light Purplish Vinaceous.

The only motor responses to handling during the first hours of nestling life (and up until about day 5.5) are a pedaling motion of the legs and a clasping and unclasping of the toes. The voice is a faint *weep-weep-weep*, uttered without opening the bill.

Subsequent development of the nestlings: endysis.—Feather development was very similar in nestlings of similar age, and the rate of growth appeared to be independent of weight variations in individual birds. It is, therefore, the best criterion of the age of the nestlings.

Day 1.5.—No conspicuous change from day 0.5; dark papillae of the contour feathers visible in the cervical region of the ventral tract in some birds.

Day 2.5.—Dark papillae visible in all tracts in which dark feathers are to appear. Papillae of the rectrices visible as a dark crescent. Sheaths of the secondaries either distending the skin of the wings (*i.e.*, "pointed"), or projecting less than 0.5 mm. through the skin.

Day 3.5.—Contour feathers of the pectoral region piercing skin of all nestlings. Sheaths of the spinal and humeral tracts beginning to pierce the skin, or at least pointed. Sheaths of the primaries either pointed or less than 1 mm. through the skin. Secondary sheaths elongating.

Day 5.5.—Pin-feather stage. Sheaths much elongated but rupturing only in the pectoral and abdominal regions. Sheaths of the rectrices less than 1 mm. through the skin. Median length of the tenth (outer) primary sheath 4.6 mm.

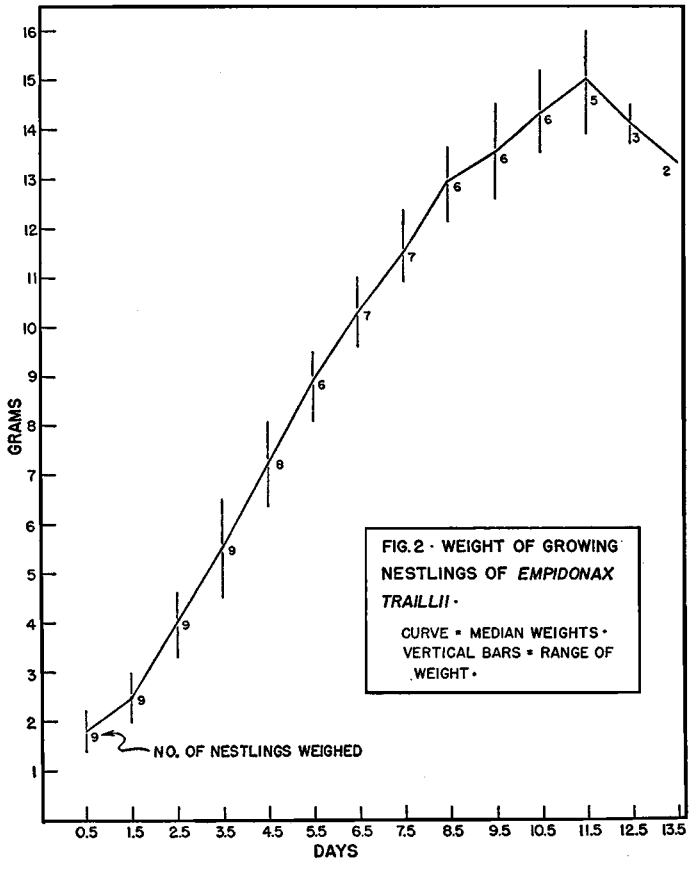


FIG. 2 · WEIGHT OF GROWING NESTLINGS OF *EMPIDONAX TRAILLII* · CURVE = MEDIAN WEIGHTS · VERTICAL BARS = RANGE OF WEIGHT ·

Day 7.5.—Vanes of most of the contour feathers well-expanded except in the frontal, gular, auricular, malar, and submalar regions. All, or nearly all, secondary vanes expanded 1 mm. or less. Sheaths of the first (inner) and second primaries may begin to rupture. Vanes of the inner rectrices expanded about 1 mm. Median length of the tenth primary sheath 10.4 mm.

Day 8.5.—The increasing exposed-vane surface gives the definitive coloration and pattern to the nestlings. All remigial sheaths now ruptured. Median length of the tenth primary sheath and vane 13.4 mm.

Day 9.5.—Wing-bars are well defined on the expanded vanes of the lesser coverts. Dorsal and lateral apteria covered by the converging contour feathers when the nestling is in repose. The ventral apterium still exposed.

Day 10.5.—Well-feathered except for frontal, auricular, gular, malar, and submalar areas, where sheaths are still prominent. Upper wing coverts cover or nearly cover the unruptured portion of the remigial sheaths, giving the wing an almost solid surface.

Days 11.5 to 13.5.—No conspicuous change in feathering. The ventral apterium is covered by the converging feathers of the ventral tract, and endysis is essentially complete in the head region by the time the young birds vacate the nest on about day 12.5.

Growth of flight feathers.—The tenth primary, of those flight feathers measured daily (*i.e.*, tenth, first primaries, outer rectrices), appears to be the only useful quantitative criterion of age (see table 3). The median growth rate of this feather in those birds measured was sufficiently rapid that the extremes of daily measurements do not overlap, although in some cases they closely approach one another. This was not true of the first primary or of the outer rectrices. No measurements of feather growth were made after day 11.5.

Daily weights of the nestlings.—The daily change in weight of the growing nestlings is shown in table 3 and figure 2. The statistical justification for using median rather than mean values for small samples is given by Dean and Dixon (1951) and will not be elaborated here. In any event, the means did not differ more than 0.3 gm. from the median values. It is readily seen, especially in figure 2, that the age

TABLE 3

WEIGHTS AND FEATHER MEASUREMENTS OF NESTLING TRAILL'S FLYCATCHERS

Day of Life	*Number of Birds*	*Median Weight*	*Range of Weight*	*Median Change in Weight*	*Length Tenth Primary*	
					Median	*Range*
0.5	9	1.8 gm.	1.4–2.2 gm.	—	—	—
1.5	9	2.5	2.0–3.0	+0.7 gm.	—	—
2.5	9	4.0	3.3–4.6	1.5	—	—
3.5	9	5.5	4.5–6.5	1.5	1.0 mm.	0.6–1.4 mm.
4.5	8	7.2	6.3–8.1	1.7 +1.5 gm./day	2.2	1.6–3.1
5.5	6	8.9	8.1–9.5	1.7	4.6	3.4–6.0
6.5	7	10.3	9.6–11.0	1.4	7.4	6.2–8.2
7.5	7	11.5	10.9–12.4	1.2	10.4	9.2–11.4
8.5	6	12.9	12.1–13.6	1.4	13.4	12.6–14.4
9.5	6	13.5	12.6–14.5	0.6	16.2	15.0–17.4
10.5	6	14.3	13.5–15.2	0.8 +0.7 gm./day	18.8	17.6–20.2
11.5	5	15.0	13.9–16.0	0.7	21.8	21.6–22.2
12.5	3	14.1	13.7–14.5	−0.9 −0.85 gm./day	NR*	NR
13.5	2	13.3	13.2–13.3	−0.8	NR	NR

*No record

of nestling Traill's Flycatchers cannot safely be determined at any stage of growth on the basis of weight. With few exceptions, the extremes of successive statistical populations overlap. In a larger sample, overlap would probably prevail in all cases and to an even greater degree.

Growth rate and motor coördination.—Three rather distinct phases of median weight change may be seen in table 3. A minor break in the data, and curve, began at about six days, when the eyes of the nestlings were opening and the birds were beginning to acquire motor reactions more complex than the gaping and grasping responses which marked the first six days of nestling life. The first cowering response to my approach was seen on day 6.5, and the wings were first used in strong

fluttering motions on this day. A sharper break in the growth-rate curve occurred on day 8, when the growth of contour feathers was substantially ended and the nestlings were generally more active. By this time the birds were able to manipulate and fold their wings quite proficiently, whereas previously the wings had hung loosely at the sides. When removed from the nest, the young birds sat erectly on their tarsi, glancing about alertly. By day 10.5, the birds were able to perch erect on my finger and shortly thereafter were using their wings in attempted escape flights from the pan of the scale. The decline in weight after day 11.5 is probably correlated with the increased activity of the young in the nest. That this decline is not an isolated case in a single brood is shown by another brood (No. 53–22) which was weighed two days prior to departure from the nest, and again on the day of departure. The first weights were 14.6, 15.0, and 15.1 gms.; the later weights were 13.4, 13.6, and 13.7 gms. At the time of the last weighing, one bird was found perched near the nest, and the other two were frightened from it. Inasmuch as their ages were not accurately known, the data are not included in table 3 or figure 2.

With due regard to minor differences in time, the sequence of development in Traill's Flycatcher does not differ markedly from that outlined by Nice (1943: 73) for open-nesting passerine species in general.

The egg tooth.—This structure is visible throughout nestling life. Its white tip is apparent to the unaided eye until about day 4.5 or 5.5. Because of the heterogonic growth of the bill, it shifts from its initial position on the culmen until, at about twelve days, it appears as a minute tubercle on the hook of the bill. It has thus rotated through 90 degrees.

The nestling period and nest departure.—Burns (1921) gives the span of nestling life in *Empidonax traillii* as 13 to 14 days. Berger and Hofslund (1950: 9) report 14 and 15 days for the species in Michigan. In my nest number 53-17, in which the nestlings were handled daily, nestlings 1 and 2, which hatched on the same day, were in the nest 12 days, 19.5 ± 4 hours. Nestling 3, which hatched a day later than its siblings, also left a day later, after 12 days, 6 ± 5 hours in the nest. These nest departures were entirely voluntary, so far as is known, and occurred during my absence. It is of course entirely possible that my daily handling of the nestlings had some effect on their tenure in the nest. Nestlings 1 and 2 were found sitting on a branch 1.5 feet from the nest, having left it between dawn and 7:30 A.M. At 6:30 P.M. they were still in the nest tree, four feet away from the nest. The following morning they were about sixty-five feet away from the nest and across a small creek, and they were being fed by the adult flycatchers. At this time nestling 3 was found perched on the edge of the nest but crouched down in it at my approach. At about 6:30 P.M. of the same day it was still in the tree but flew out of it as I approached, alighting about forty-five feet away. It is evident that this species acquires some degree of proficiency in flying within a day after leaving the nest.

Reproductive success.—Of 33 clutches, 19 were of three eggs, and 14 were of four eggs. This ratio differs from the data of Berger and Hofslund (1950), who found nine clutches of three eggs and 14 clutches of four eggs in 23 nests in Michigan, and from Farley's (1901) report that clutches of four eggs are the more common in eastern Massachusetts. During the first year of the present study, 21 of 25 eggs hatched, a success of 84 per cent. In 1953, 42 of 43 eggs hatched, a success of 98 per cent. Berger and Hofslund (1950) report a hatching

success of 92 per cent for 36 Traill's Flycatcher eggs. I have no satisfactory data for fledging success in the Palouse Hills in 1952, but in 1953, it was 44.6 per cent (21 of 47 nestlings were successfully fledged). This is quite close to the average fledging success of 43.0 per cent which Nice's (1937: 143) compilation indicates is typical of passerine species which construct open nests.

Causes of nesting failure were known in only a few cases. Two nests contained one Brown-headed Cowbird egg each. One of these was abandoned by the flycatchers before incubation began, and the nestlings in the other nest, which hatched when the cowbird was about three days old, would not have survived, judging from their almost static daily weights, even if a predator had not taken them. Cattle trampled two nests, and Black-billed Magpies (*Pica pica*), attracted to the study area in rather large numbers by rodents killed in a nearby wheat fire, are suspected of having taken several sets of eggs. Only one case of malformation was observed in the 60 nestlings examined during the course of this study. This bird lacked the left one-half of the upper mandible from the nostril distad. It was as far advanced as its nest mates and resisted handling just as vigorously. A very dense population of the Northern Fowl Mite (*Bdellonyssus sylvarium* C. and F.) was found in one nest. A nestling about twelve days old was collected from this nest, and despite the heavy infestation of mites, the bird seemed healthy and was of normal weight.

Voice.—Two general song types are attributed to *Empidonax traillii* in the eastern and midwestern portions of its range; a bi-syllabic form usually transcribed as *fitz-bew*, and a tri-syllabic type designated by *way-be-o* or *phe-be'-o* (Aldrich, 1953; McCabe, 1951). Allen (1952), in commenting upon certain phonetic transcriptions of the songs, correctly points out that syllabification is the result of human interpretation and transcription of the component sounds of the song and that some hearers may regard as a discrete syllable what others interpret merely as an inflection. Nevertheless, experienced field observers are agreed that two different songs exist in eastern (three syllables) and midwestern (two syllables) populations, and their opinions have been confirmed to a certain extent by audiospectrography (Kellogg and Stein, 1953).

Table 4 summarizes some interpretations of calls appearing in western literature. Regrettably, only a few of these can be closely fixed with regard to locality. In preference to arranging these calls according to syllabification, they have been classed on the basis of their apparent resemblance to a *deer* or a *bew* sound. As will be pointed out below, these phonetic groupings are ones into which the extensively

recorded calls of *Empidonax traillii* in the Palouse Hills fall rather conveniently, if not naturally. Further, as Aldrich (1953: 9) suggests, the "quality" of the song, as well as syllabification, may be a profitable avenue of investigation in comparing racial affinities and differences. This paper attempts to emphasize the two phonetic and syllabic groupings, together with their "quality" as expressed in the phonetics and manner of delivery of the calls, which are rendered by birds in the Palouse Hills and perhaps in the western United States in general.

TABLE 4

PHONETIC TRANSCRIPTIONS OF THE SONGS OF *Empidonax traillii* IN THE WEST

Song	*Authority*	*Locality*
Based on *deer* sound		
Weeps-a-dee-ar	Sumner and Dixon (1953)	Sierra Nevada
Weep-a-de'-ar	Peterson (1941)	Western U. S.
Weeps-a-pi-de'ea	Hoffmann (1927)	Pacific States
Pree-pe-deer	Cooke (*in* Bailey, 1915)	Western U. S.
Pre-pe-dee'	Howsley (*in* Bent, 1942)	Western Washington
We're he're	Taverner (1926)	Western Canada
Pi-de'ea	Hoffmann (1927)	Pacific States
Week tse weer!	Jewett, *et al.* (1953)	Washington
Reek rair!	Jewett, *et al.* (1953)	Washington
Based on *bew* sound		
Fitz-bew	Peterson (1941)	Western U. S.
Fitz-be'-o	Peterson (1941)	Western U. S.
Fay-be'-o	Peterson (1941)	Western U. S.
Prets-kew!	Jewett, *et al.* (1953)	Washington
Whitch-koo whitchy-koo!	Jewett, *et al.* (1953)	Washington
Zwee'bew, zzweet	Dawson and Bowles (1909)	Washington
Zwee'bew, zzweet	Dawson (1923)	California
Not classified		
Zwee'-beck	Howsley (*in* Bent, 1942)	Western Washington
Ezee-e-u'p	Taverner (1926)	Western Canada
Rrrynk!	Jewett, *et al.* (1953)	Washington
Preet!	Jewett, *et al.* (1953)	Washington

In common with certain of its midwestern relatives, Traill's Flycatcher in the Palouse Hills sings a distinctly two-syllabled song, *during the nesting season.* This is quite recognizable as the *fitz-bew* type of authors but to my ear is phonetically best transcribed as *whitz'-bew,* delivered explosively. This call has minor variations described below. When Traill's Flycatchers first appear in the spring, however, they utter a *distinctly three-syllabled* call which I have repeatedly recorded as *whip'-a-deer* and *weeps'-a-deer.* This tri-syllabic call is heard concurrently with the *fitz-bew* type, but as the courting season wanes it is heard less and less frequently until (except under conditions described below) it gives way almost entirely to the bi-syllabic form. Although this call is delivered emphatically, it does not have the explosive vigor of the *whitz'-bew* call. Howsley (*in* Bent, 1942: 203)

also noted a seasonal difference in the song of Traill's Flycatcher in Washington, recording the early call as *pre-pe-dee'*, and the later one as *zwee'-beck*. Saunders (*in* Aldrich, 1953: 8) reports a similar seasonal change in syllabification in eastern populations of *Empidonax traillii*. It is remotely possible, of course, that the migrant members of a more northern population, to which a tri-syllabic call is peculiar, are responsible for an apparent seasonal song dimorphism. However, certain features of the quality and phonetics of the call and of its occurrence lead me to believe that this is not the case. First, the *whip'-a-deer* call is employed by birds in territorial dispute early in the season. On 15 June 1953, I observed three males contending for portions of a small willow thicket. Each of them used this call repeatedly and vigorously. It is extremely doubtful that birds at this late date and engaged in this activity would be migrants. Secondly, the *whip'-a-deer* call, and variants using the *deer* sound, may be heard throughout the nesting season. I have failed to detect the exact circumstances which induce the tri-syllabic call but have noticed that on the few occasions when a male was stimulated to vocalization by the presence of an observer at its nest, this was the call generally employed.

Calls recorded for the Palouse Hills' population of *Empidonax traillii* appear in table 5. In interpreting and transcribing these calls in the field, every effort was made to avoid classifying them into conventionalized forms.

TABLE 5

PHONETIC TRANSCRIPTIONS OF THE SONGS OF TRAILL'S FLYCATCHER IN THE PALOUSE HILLS

Basic Song or Call	*Variations*
Based on *deer* sound	
1. *Whip'-a-deer*	1a. *Pi-dee'r*
2. *Whit'-spdeer*	2a. *Whit'-spdee*
3. *Whip's-deer*	
Based on *bew* sound	
4. *Whitz'-bew*	4a. *Writz'-ew*
5. *Whrrit'-ew*	5a. *Whrrit*
6. *Whree'-ew*	6a. *Whree'-o*
Call notes	
7. *Whip!*	7a. *Wheet!*

To that end, daily records were kept separate and were not collated or reviewed until the song season ended. The transcriptions appearing in table 5 are in the same form that they were recorded in the field. Because of the situation at the Missouri Flat Creek study plot, where many of the records were obtained, it was possible to compare the

calls of birds in the creek bottom with those inhabiting hillside thickets some 150 to 300 yards distant, thus noting the effect of distance and possible differences in birds of those dissimilar habitats. Also, because of the relatively dense population of the species in the creek bottom, song variations of one sort could immediately be compared with those of another type, thus reducing to a minimum the variable of what may be called "auditory memory."

In table 5 it may be seen that a *whip* or *whitz* element, together with an accented first syllable, is the common denominator in all calls except 1a. Song 1 is the definitely tri-syllabic type heard frequently early in the season. The *pi-deer'* call (1a) is also most frequently heard early in the season. Songs 2, 2a, and 3 are intermediate in syllabification and emphatic quality. It is often impossible to assign a call to a distinctly bi- or tri-syllabic category. Songs 4, 4a, and 5 are based on the *bew* note and are characteristic of the twilight song periods. Call 5a has a burry, grating quality and is delivered with an abrupt upward inflection. It is apparently homologous with Hoffmann's (1927) *prrit*, the *rrrynk!* and *preet!* of Jewett, *et al.* (1953), and McCabe's *creet* note, but it lacks the clear tonal quality implied by these latter two transcriptions. It does not enter into any consistent song pattern. Song 6 is a type which is infrequently heard at twilight. Like the *whrrit* call, it has a grating quality, with the *-o* or *-ew* element muted. Calls 7 and 7a are typical call notes. It seems to be a case of individual variation whether the note is of a flat tone (7), or whether it has a certain musical quality (7a), but the emphatic *whip!* type is by all odds the more common.

In final analysis, all that can be determined regarding song types by these observations is that: 1) The tri-syllabic *whip'-a-deer* call is confined chiefly to the pre-nesting season, 2) the *deer* element of the early song is present in several variations throughout the breeding season, and, 3) the calls given during the twilight song periods are based principally, if not exclusively, on the *bew* sound. It should be noted, however, that the *whit'-spdeer* type is also occasionally heard during the "tuning-up" phase which typically precedes the evening song period proper. A typical series, recorded on 18 July 1953, was: *whit!, whit!, whit!, whit'-spdeer, whit'-spdee* (pause) *whit!, whit!, whitz'-bew, whrrit!, whitz'-bew!* It remains to be demonstrated what correlation, if any, exists between song-type and the chronology of the breeding season. To this end, it would be interesting to have additional and more detailed information from other western populations of *Empidonax traillii.*

Song periodicity and song perches.—Traill's Flycatcher is already

in song when it arrives in the Palouse country in late May or early June. During 1953, regular evening song periods continued until the first week of August, when the theretofore well-defined song periods became sporadic. They ceased entirely on about 10 August, after which no birds were heard in regular twilight song, even though a few pairs still were attending young in the nest. Because of limited time afield, I have little data on diurnal song periodicity. However, some of it is interesting for comparative purposes. On 4, 5, and 6 July, morning song began abruptly at about 3 A.M. (P.S.T.). Traill's Flycatcher was the earliest species heard in the morning and was joined after a few minutes by the Western Flycatcher (*Empidonax difficilis*) and the Willow Thrush (*Hylocichla fuscescens*). Aside from an abrupt beginning, the morning song period was ill-defined, continuing intermittently until about 9:30 A.M. Comparatively few Traill's Flycatchers are heard during midday except in infrequent territorial disputes.

The limits of the evening song period are quite sharp, and except for a few individuals which call "prematurely," the birds of a given area begin and stop singing almost in unison. In common with McCabe (1951), I experienced little difficulty in assigning definite limits to the evening song period. On 25, 27, 30 July, and 2 August, the duration of this period was, respectively, 31, 33, 65, and 31 minutes. The weather was clear and warm on all of these days, and there is no readily apparent reason for the prolonged period on 30 July. Except for 25 July, when the evening song period extended 15 minutes beyond the end of civil twilight, the cessation of song fell within three minutes of the end of civil twilight. This is quite at variance with McCabe's (1951) much more extensive data, which indicate the evening song period consistently extends farther beyond twilight in Wisconsin.

The principal song perches of the males during the twilight period are the bare twigs at the tops of a hawthorn or chokecherry bushes, 12 feet to 30 feet above the ground, or, in the more barren uplands, on a telephone wire. During the "tune-up" period previously mentioned, the males flit from perch to perch, often feeding en route, building up to the crescendo of *whitz'-bew* calls which characterizes the twilight period, until they have attained an exposed site, which is frequently the highest bare twig in their territory. As a rule, they do not move from this site, except to snap up a passing insect, for the duration of the song period, although they occasionally move to a similar nearby perch. I have not witnessed the "song-flight" described by McCabe (1951), but this does not preclude the possi-

bility of its occurrence. From the best available vantage point I was able to observe only two singing birds at one time. Calls per minute, timed for three different males over 18 consecutive minutes at the height of the twilight song period, averaged 12.7. This included only distinct *whitz'-bew* calls and not the almost incessant *whit* and *whrrit* notes which accompany them.

Behavior of the Adults.—In contrast to many reports, I have not found Traill's Flycatcher in the Palouse Hills to be excessively shy in the presence of humans *except* after the nesting season is completed and territories have been abandoned. During this period they are rather furtive, and it is necessary to "call them in" by making squeeking sounds with the lips. To this artifice they usually respond only once. During the spring and the nesting season, however, feeding birds take no heed of the observer until he is within about thirty feet of them. Even then they rarely seek refuge but are as likely to move further away and continue feeding. Very much in contrast to what is said of eastern populations (Farley, 1901: 354; Bent, 1942: 209), *E. t. brewsteri* is a quite close sitter. Indeed, one of the more profitable means of locating nests is to agitate the brush and watch for a departing female. The behavior of the adults when an observer is at the nest varies widely with individual pairs and has no evident correlation with the chronology of the reproductive season. Some females, after flushing, are not seen or heard again; others skulk in the brush nearby uttering their *whit* or *wheet* note. Still others flush from the nest to an exposed perch where they sit, *whit*-ing constantly. A few females are particularly aggressive and fly at the intruder vigorously snapping their beaks, *whit*-ing furiously, and flitting back and forth near the nest in great agitation. Occasionally, a male will become infected with the excitement of its mate and accompany her to the nest, calling *whitz'-spdeer*.

In its feeding habits, Traill's Flycatcher is quite conspicuous, and the birds seek an exposed perch from about one foot to about eight feet above the ground. Singing males frequently feed from their song posts, but at other times during the diurnal cycle they are not often observed above the heights indicated. Although perch predilection is no doubt determined to a certain extent by the height at which flying insects are most abundant, typical feeding perches are seen to be the strands of fences, a bare twig overhanging a steep-cut creek bank, or one of the many dead branch-ends provided by the peripheral foliage of the hawthorn. Occasionally, a Traill's Flycatcher may be observed feeding along the edge of a wheatfield, flitting rapidly from spike to spike or darting out almost at ground

level over an open meadow, poising momentarily on slender herbaceous stems.

SUMMARY

The area in which Traill's Flycatcher was studied lies in southeastern Washington in the broad ecotone between the Palouse grassland and the conifer forest of the northern Rocky Mountains. The aboriginal vegetation of this area has been greatly reduced by agriculture, and the habitat of Traill's Flycatcher is now confined to narrow streamside thickets, restricted upland prairie remnants, and the brushlands fringing coniferous forest.

In the Palouse Hills, Traill's Flycatcher occurs both in relatively mesic riparian thickets *and* dry upland brush patches. This habitat distribution is similar to that reported for *Empidonax traillii* in the East and Midwest but differs from the majority of reports from the West, which strongly emphasize an affinity for dense cover and moist areas.

Certain factors apparently important in determining the habitat distribution of Traill's Flycatcher in the Palouse Hills are discussed.

The site and structure of 42 Traill's Flycatcher nests are analyzed. Yellow Warbler-like nests and Song Sparrow-like nests form the extremes of a series which includes intermediate types.

The chronologies of the nesting seasons of 1952 and 1953 are discussed in relation to plant phenology and other factors.

The growth of four broods of Traill's Flycatchers is analyzed in terms of weight, endysis, and behavioral development. Of those measurements taken, the length of the tenth primary proved to be the only single reliable criterion of the age of the nestlings.

Hatching success during 1952 was 84 per cent. During 1953, it was 98 per cent. Fledging success during 1953 was 44.6 per cent.

The voice of Traill's Flycatcher in the Palouse Hills is compared with phonetic transcriptions appearing in the literature. During the courting season in this area, a three-syllabled song predominates, giving way in the nesting season to a two-syllabled song. The songs and their variations fall rather naturally into two groups: those including a *bew* note and those including a *deer* note. The call notes comprise a third group.

Traill's Flycatcher was found to be a rather close sitter at the nest, and often an agressive defender of it; but this latter behavior varied greatly with individual females.

LITERATURE CITED

ALDRICH, J. W. 1951. A review of the races of the Traill's Flycatcher. Wilson Bull., **63:** 192–197.

ALDRICH, J. W. 1953. Habits and habitat differences in two races of Traill's Flycatcher. Wilson Bull., **65:** 8–11.

ALLEN, F. H. 1952. The song of the Alder Flycatcher. Wilson Bull., **64:** 107–109.

BAILEY, F. M. 1915. Handbook of birds of the western United States, Fourth Edition. Houghton Mifflin Co., Boston.

BEECHER, W. J. 1942. Nesting birds and the vegetation substrate. Chicago Ornithological Society.

BEHLE, W. H. 1943. Birds of the Pine Valley Mountain region, southwestern Utah. Bull. Univ. Utah, **34:** 1–85.

BENDIRE, C. 1895. Life histories of North American birds. Smiths. Inst. Spec. Bull. 3.

BENT, A. C. 1942. Life histories of North American flycatchers, larks, swallows, and their allies. U. S. Natl. Mus. Bull. 179.

BERGER, A. J., and P. B. HOFSLUND. 1950. Notes on the nesting of the Alder Flycatcher (*Empidonax traillii*) at Ann Arbor, Michigan. Jack-pine Warbler, **28:** 7–11.

BERGER, A. J., and D. F. PARMELEE. 1952. The Alder Flycatcher in Washtenaw County, Michigan: breeding distribution and cowbird parasitism. Wilson Bull., **64:** 33–38.

BURNS, F. L. 1915. Comparative periods of deposition and incubation of some North American birds. Wilson Bull., **27:** 275–286.

BURNS, F. L. 1921. Comparative periods of nestling life in some North American Nidicolae. Wilson Bull., **33:** 90–99.

CAMPBELL, L. W. 1936. An unusual colony of Alder Flycatchers. Wilson Bull., **48:** 164–168.

DAWSON, W. L. 1923. The birds of California. South Moulton Co., San Diego.

DAWSON, W. L., and J. H. BOWLES. 1909. Birds of Washington. Occidental Publ. Co., Seattle.

DAUBENMIRE, R. F. 1942. An ecological study of the vegetation of southeastern Washington and adjacent Idaho. Ecol. Monogr., **12:** 53–79.

DEAN, R. B., and W. J. DIXON. 1951. Simplified statistics for small numbers of observations. Analyt. Chem., **23:** 636–638.

DUMAS, P. C. 1950. Habitat distribution of breeding birds in southeastern Washington. Condor, **52:** 232–237.

FARLEY, J. A. 1901. The Alder Flycatcher (*Empidonax traillii alnorum*) as a summer resident of eastern Massachusetts. Auk, **18:** 347–355.

FISHER, L. C. 1941. Supplementary climatic notes for Washington. Yearbook of Agric., pp. 1170–1181.

GABRIELSON, I. N., and S. G. JEWETT. 1940. Birds of Oregon. Oregon State College, Corvallis.

GRINNELL, J., and A. H. MILLER. 1944. The distribution of the birds of California. Pac. Coast Avifauna No. 27.

HAND, R. L. 1941. Birds of the St. Joe National Forest, Idaho. Condor, **43:** 220–232.

HOFFMANN, R. 1927. Birds of the Pacific States. Houghton Mifflin Co., Boston.

HUDSON, G. E., and C. F. YOCOM. 1954. A distributional list of the birds of southeastern Washington. Research Studies State Coll. Wash., **22:** 1–56.

JEWETT, S. G., W. P. TAYLOR, W. T. SHAW, and J. W. ALDRICH. 1953. Birds of Washington State. Univ. Wash. Press, Seattle.

KELLOGG, P. P., and R. C. STEIN. 1953. Audio-spectrographic analysis of the songs of the Alder Flycatcher. Wilson Bull., **65**: 75–80.

LACK, D. 1933. Habitat selection in birds. Jour. Anim. Ecol., **2**: 239–262.

LACK, D. 1950. The breeding seasons of European birds. Ibis, **92**: 288–316.

LACK, D., and E. T. SILVA. 1949. The weight of nestling robins. Ibis, **91**: 64–78.

LEOPOLD, A. 1936. Game Management. C. Scribner's Sons, New York.

LEOPOLD, A., and S. E. JONES. 1947. A phenological record for Sauk and Dane counties, Wisconsin, 1935–1945. Ecol. Monogr., **17**: 81–122.

MCCABE, R. A. 1951. The song and song-flight of the Alder Flycatcher. Wilson Bull., **63**: 89–98.

MEANLEY, B. 1952. Notes on the nesting of Traill's Flycatcher (*Empidonax traillii*) in southeastern Arkansas. Wilson Bull., **64**: 111–112.

MILLER, A. H. 1941. A review of centers of differentiation for birds in the western Great Basin region. Condor, **43**: 257–267.

NICE, M. M. 1937. Studies in the life history of the Song Sparrow, I. Trans. Linn. Soc. N. Y., **4**.

NICE, M. M. 1943. Studies in the life history of the Song Sparrow, II. Trans. Linn. Soc. N. Y., **6**.

OBERHOLSER, H. C. 1932. Descriptions of new birds from Oregon, chiefly from the Warner Valley region. Sci. Publ. Cleveland Mus. Nat. Hist., **4**: 1–12.

PETERSON, R. T. 1941. A field guide to Western birds. Houghton Mifflin Co., Boston.

PHILLIPS, A. R. 1948. Geographic variation in *Empidonax traillii*. Auk, **65**: 507–514.

RIDGWAY, R. 1912. Color standards and color nomenclature. Washington, D. C.

SNYDER, L. L. 1953. On Eastern Empidonaces with particular reference to variation in *E. traillii*. Contrib. Royal Ontario Mus. Zoöl. and Paleontology **35**.

STEVENSON, E. 1942. Key to the nests of Pacific Coast birds. Oregon State Monogr., Studies in Zoöl., 4.

SUMNER, L., and J. S. DIXON. 1953. Birds and mammals of the Sierra Nevada. Univ. Calif. Press, Berkeley and Los Angeles.

TAVERNER, P. A. 1926. Birds of western Canada. Bull. Nat'l Mus. Canada, 41.

TREASHER, R. C. 1926. Stratigraphic aspects of loess of Palouse region. Pan-Amer. Geol., **46**: 305–314.

UNITED STATES DEPARTMENT OF COMMERCE, WEATHER BUREAU. 1953. Climatological data, Washington section, **57** (3–7).

WING, L. 1949. Breeding birds of virgin Palouse prairie. Auk, **66**: 37–40.

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