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ON EASTERN EMPIDONACES WITH PARTICULAR
REFERENCE TO VARIATION IN *E. TRAILLII*

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INTRODUCTION AND ACKNOWLEDGMENTS

THE PRESENT STUDY is in fact an outgrowth of an attempt to classify four specimens of *Empidonax* collected on Pelee Island (Lake Erie), Ontario, in 1950. Obviously these specimens did not conform with *Empidonax traillii* from throughout northern Ontario with which the writer was most familiar. In order to resolve a local question of this kind, involvement in *Empidonax* taxonomy was inescapable and some matters of broader concern have accrued. Approximately 400 specimens of *E. traillii* have been examined, as well as many additional specimens of closely allied forms, particularly from the east. This Museum's collections have been amplified by the loan of pertinent specimens from the National Museum of Canada, through Mr. W. Earl Godfrey; the University of Michigan Museum of Zoology, through Dr. J. Van Tyne; the Ohio State Museum, through Dr. Edward S. Thomas; and the Cleveland Museum of Natural History, through Mr. William E. Scheele. Thanks are extended to these institutions and individuals.

COMPARISONS OF SPECIES

Size: In nuptial plumage two species of *Empidonax* in the east, *E. minimus* and *E. virescens*, are frequently difficult to distinguish from *E. traillii*. Size constitutes a useful taxonomic character, yet there is overlap between *E. traillii* and *E. minimus*, and a wider overlap between *E. traillii* and *E. virescens*. For comparison, the minimum and maximum measurement of one feature, chord of wing, are given for males, as are also the measurements of the species irrespective of sex. The measurements are in millimeters and the sources of the data are inserted: For *E. traillii*, ♂♂, 64.5 to 78 (Ridgway, 1907, p. 558); for *E. minimus*, ♂♂, 59 to 67 (Ridgway, *op. cit.*, p. 562); and for *E. virescens*, ♂♂, 68.3 (personal) to 80.5 (Ridgway, *op. cit.*, p. 553). If statistics for both sexes are combined a still wider overlap is evident: For males and females of *E. traillii*, 60.7 (Phillips, 1948, p. 511) to 78 (Ridgway, *op. cit.*, p. 558); for *E. minimus* (no change, females relatively larger); and for

E. virescens, 67.5 to 80.5 (Ridgway, *op. cit.*, p. 553). There might be some doubt as to the advisability of combining the measurements from different sources but variation in method of measurement by students of *Empidonax*, could not be sufficiently wide as to materially disturb the thesis of size overlap. With respect to the possibility of wrongly sexed specimens there is no infallible check on a collector's datum. The critical figure in the comparison made would be the minimum male measurement of *E. traillii* as given by Ridgway. Phillips (*loc. cit.*) gives a minimum of 66 which is but 1.5 larger. Comparative wing measurements for males and for the combined sexes are shown graphically in fig. 1. Similar overlaps occur in other measurements, including length of culmen, tail, total length, wing spread, and weight, so that size is not an absolutely diagnostic specific character.

FIG. 1. Minimum and maximum chord of wing measurements (in millimetres) for three species of eastern *Empidonax*:

- A. Intra-species variation and comparative inter-species variation, males only.
- B. Intra-species variation and comparative inter-species variation, sex not distinguished.

One measurement has been found particularly useful in distinguishing *E. traillii* from *E. virescens*. The length of the wing tip, i.e., the distance from the tip of the secondaries in the folded wing to the end of the longest primary, is usually diagnostic. This character, pointed out long ago by Baird (1858, p. 197) was investigated with the following results: In a series of 37 males of *E. virescens* the measurements were 16.0 minimum

and 23.5 maximum, with an average of 19.3 ± 0.27 . The measurements from a series of 20 males of *E. traillii* originating from within the geographic range of *E. virescens* were 12.0 to 17.5 with an average of 14.2 ± 0.29 . The five millimeter difference in the averages of the length of wing tip (actually 5.1 ± 0.43), is therefore useful in distinguishing males of *E. traillii* and *E. virescens*. The situation is similar for females as follows: 13 *E. virescens*, 15.0 to 20.0 (av. 17.3 ± 0.43) and 16 *E. traillii*, 10.5 to 17.0 (av. 12.8 ± 0.50); difference, 4.9 ± 0.68 .

Colour: Nuptial plumage colour is a helpful but not an infallible character in distinguishing these three species of *Empidonax*. Though the species *E. minimus* and *E. virescens* show little variation in dorsal colour, *E. traillii* varies markedly, both geographically and, to some extent, individually, in some areas. The green of the back may be sufficiently warm to match or exceed that of *E. minimus*. The colder dorsal green which characterizes the nuptial plumage of *E. virescens* seems never to be overlapped by *E. traillii*, yet selected specimens show that they converge very closely indeed. There is a wide range of ventral colour in *E. traillii*, from nearly white to primrose yellow. More diluted or colourless examples overlap the ventral colour range of both *E. minimus* and *E. virescens*. The horn brown colour of the upper mandible and feet of museum specimens of *E. virescens* may distinguish this species from certain geographic representatives of *E. traillii* and from *E. minimus* which have black upper mandibles and feet, but it has been observed that this colour on *E. virescens* can be matched by representatives of *E. traillii* from the far west. Colour of wing bars is somewhat variable in all three forms but is most variable in *E. traillii*. This marking is weakest and most drab in Pacific *E. traillii* and most colourful, olive buff, in the same species elsewhere. Colour, like size, therefore, is not a character with clear-cut diagnostic value in distinguishing these species.

Pattern: Pigment pattern is to some extent an aid in distinguishing these three species of *Empidonax* in nuptial plumage. The breast band is a case in point. This pattern is about equally vague in *E. minimus* and *E. virescens*. In *E. traillii* it is found to vary from weak to strong. Partly as a result of contrast with the breast band and partly as a result of the absence of pigment, the throat of *E. traillii* appears whiter, on the average, than does this area on the other two species, but this pattern cannot be relied upon for specific identification.

Shape: Two characters found to be helpful in distinguishing the three species here concerned have to do with the outline or shape of the termination of both the wing and tail. The end of the tail in mature *E. traillii* and *E. virescens* is usually rather even, occasionally very slightly rounded. More rarely the central feathers are slightly shorter, imparting an emarginate effect. In *E. minimus* the termination is usually emarginate, owing to the slightly shorter central feathers, and sometimes slightly double rounded when the outer feathers do not equal the longest.

The shape of the wing tip is also of value in specific diagnosis. In detail this character concerns the length of the tenth (outer) primary in relation to the length of the fifth primary ("sixth", counting from the distal end). In *E. minimus* the tenth is equal to, or shorter than, the fifth; in *E. virescens* the tenth is much longer than the fifth, sometimes longer than the sixth ("fifth"). In *E. traillii*, geographic forms considered collectively, the situation encompasses that found in the other two species, western populations being like *E. minimus* and eastern populations like *E. virescens*.

Preference with respect to ecological niche: Certain biological characters helpful in distinguishing these three species of *Empidonax* are non-morphological. The choice of ecological niche for nesting is a biological character of this kind. Apparently *E. virescens* displays the narrowest choice of the three. It seems to be strictly a bird of mature, moist forests, from cypress swamps to beach-maple climax, in bottomlands and ravines. Both *E. minimus* and *E. traillii* display a wider choice. On the whole, both prefer forest edge, or opening conditions in wooded wilderness areas, and *E. traillii* is adapted to non-forested sections of the continent.

In more detail, *E. minimus* occupies alder thickets, those bordering streams or covering low topographic basins. It is also found in dry terrain, in well developed birch copses, in fairly mature stands of aspen poplar, and, locally, in young second-growth hardwood. In some cultivated districts it has invaded orchards and shade trees about habitations. The choice of *E. traillii* is variable, though its major habitat is alder or willow (or both) overgrowing wet swales. However, it occupies dry semi-clearings with young, low stands of aspen poplar, dry pastures with scattered and clumped bush, and orchards, cemeteries and shade trees about habitations in some districts. Locally the species may be found in close association with *E. minimus*, thus erasing any sharp distinction between the

ecological choice of the two, but rarely does either invade the niche of *E. virescens*.

The proclivity of *E. traillii* to inhabit both dry and wet situations, a matter which will be emphasized later, is not without parallel among birds, even the *Tyrannidae*. *Tyrannus tyrannus* is an inhabitant of orchards, hedgerows, and hawthorn-dotted drylands in the south. In the north it shows a distinct preference for tamarack bogs and the drowned shores of lakes and rivers. The common factor between these extremes, beyond the semi-open or edge conditions, is not readily perceived. Certainly numerous edge conditions within the range of the species are not occupied.

Colonizing: No evidence has been discovered to indicate that *E. minimus* tends to colonize for nesting. However, *E. traillii* displays a marked tendency to do so (Berger and Parmelee, 1952). Close association is not merely enforced by restricted or insular ecological conditions as attested by the rather wide range of choice exhibited by this species and by the extensiveness of apparently suitable but unoccupied habitat. *E. virescens* is usually regarded as solitary, and any occurrence in groups may well be accounted for by the restriction of favourable conditions locally.

Song: The vocal utterances of the three species of *Empidonax* under discussion constitute quite distinctive biological characteristics which can be considered heritable. Mechanically recorded sound recordings offer the only accurate basis for comparisons but a general discussion will reveal certain features of their full and regular songs, i.e., not including alarm notes, flight songs, etc. No one has ever suggested that the 'chebec' (accent on the last syllable) of *E. minimus* resembles any variation of the song of either of the other two. Griscom (1923, p. 236) states that *E. virescens* has two songs, "both violent sneezes. One of two syllables has the accent on the *first*. Another of three with the accent on the *last*." Undoubtedly there is more variation in the song of *E. traillii* than in either of the other two species. Notwithstanding variation in the perception of ornithologists and also in their aptitude for onomatopoeia, variation in the song of this species is obvious. Continentally, the song of *E. traillii* ranges from 'pree-pe-deer' or 'brigadier' (in the west) through 'zweebeo' or 'phe-be-o' or 'zweebie' to 'witziu' or 'fitz-bew' or 'pit-too' (in the north and east). On Pelee Island (and possibly on Point Pelee) the song of *E. traillii* is an explosive sneeze, 'witziu', with the accent on the first syllable. This song is

deceptively like one of the songs of *E. virescens*, at least as the latter sings at Rondeau Park (on Lake Erie) Kent County, Ontario. This similarity has been noticed by Mr. J. L. Baillie, Mr. F. H. Emery, Dr. Wm. W. H. Gunn, Mr. Geo. W. North, and Dr. Keith Reynolds, all of whom have heard the songs of both species in the places mentioned, and whose combined impressions leave no room for doubt.

In general terms, then, song is useful, in fact one of the most useful characteristics employed in identifying the species of *Empidonax* in life, but there is some chance of confusion, at least locally, between *E. traillii* and *E. virescens*.

Nest: The nests of *E. minimus* and *E. virescens* are quite unlike, and each is fairly constant with respect to the nature of material used, the architectural form, and the nature of the immediate situation where built. Illustrations of the compacted cup (in a fork of a small or large tree) of *E. minimus* are given by Bent (1942, pl. 27 and 28). The more shallow, semi-pensile loose basket of *E. virescens*, situated on a horizontal support, even drooping branches and twigs, is also figured by Bent (*op. cit.*, pl. 23 and 24). Nests of *E. traillii* are also figured by Bent (*op. cit.*, pl. 25 and 26). Although this species generally builds its nest in the fork of a shrub or small tree, there is variation in height from the ground, architectural appearance, and in materials used. The latter cannot be explained on the basis of availability, and may well represent an inherent difference. The two extremes are as follows: One is a compact, felted cup (lower figure, Bent's pl. 25) which resembles somewhat the nest of *E. minimus* (Bent's pl. 28) but is even more like the nest of the Yellow Warbler, *Dendroica petechia*; the other may be termed sparrow-like, compact internally but outwardly untidy, often with straw streamers from the sides and bottom (Bent's pl. 26 and Mousley, 1931, pl. 14).

The foregoing summarizes differences among the three eastern species of *Empidonax* under discussion—*minimus*, *traillii* and *virescens*—and emphasizes particularly their close similarities. No attempt has been made to make comparisons of eggs and juvenal and winter plumages. The morphological differences observed are slight and largely a matter of degree. The most striking differences are found among non-morphological characteristics. In spite of close morphological similarity and even wide overlap of many characters, no ornithologist would question their specific rank. Each is identifiable by a combination of attributes—size, colour, pattern, shape, niche preference, gregariousness, song, nest and geographic range.

GEOGRAPHIC VARIATION IN *E. traillii*

In Ridgway's early classification of *Empidonax* (*op. cit.*, p. 546) the length of the tenth primary in relation to the fifth was used to divide the genus into two groups of species. Moore (1940, p. 350) points out that more recent investigations show that the character is not distributed in this way. Phillips (1944) emphasizes its usefulness in racial studies within the species, *E. traillii*. He states that "in *E. t. traillii*, the outer primary is normally a little longer than, or equal to, the fifth; but in *E. t. brewsteri* it is almost invariably shorter than the fifth."

In examining a series of specimens of *E. traillii* (57) from the west (from southwestern British Columbia south to Baja California, and east to northeastern Utah, extreme southwestern Wyoming, western Montana, and the border of southwestern Alberta) the writer finds the wing formula, tenth primary shorter than the fifth, to be characteristic, as stated by Phillips. Populations displaying this formula include at least three currently recognized races (Aldrich, 1951) namely *E. t. brewsteri*, *E. t. extimus* (to which the northeastern Utah specimens have been assigned by the writer) and *E. t. adastus*. The postulated race *E. t. zopholegus* (Oberholser, 1947) has been rejected by Aldrich (*op. cit.*) and some doubt has been cast on *E. t. adastus* (of Oberholser, 1932; p. 3) by Miller (1941, p. 259). The few *adastus*-like birds examined by the writer, from interior British Columbia and the southwestern border of Alberta, are greener (less brown) dorsally than coastal birds, but have the western wing formula. Asymmetry of the wings, i.e., "western" on one and "eastern" on the other, observed in two specimens from southwestern Alberta, their greenish colour and the intermediate geographic source suggests a hybrid origin between southwestern and northeastern populations.

Eastern populations, including the north, usually are characterized by the tenth primary being longer than the fifth. In fact, the figures for a series of 67 northern males show the tenth primary to be longer than the fifth in 100% of cases; equal to the sixth in 12% and actually longer than the sixth in 4% of the specimens. A series of 15 females from the same region show the tenth primary to be equal to the fifth in approximately 13%, and longer than the fifth in approximately 87%. Southern populations in the east show agreement in this regard. We can therefore divide *E. traillii* geographically into two sections on this character as represented in fig. 2. In view of the limited number of western specimens examined, the boundary between the two should be regarded only as an approximation.

FIG. 2. ——— 10th (outer) primary shorter than the
 ——— fifth (= "6th" from the outside),
 ——— rarely equal to it.
 ||||| 10th (outer) primary longer than the
 ||||| fifth (= "6th" from the outside),
 ||||| rarely longer than the sixth
 ||||| (= "5th" from the outside).

A brief history of the taxonomy of eastern E. traillii: Studies concerned with geographic variation of eastern *E. traillii* have brought about a number of interpretations and proposals. The postulated *E. ridgwayi* (Sclater, 1888, pp. 222 and 227) based on a specimen from Bogota, Colombia, has been shown to be invalid (van Rossem, 1934) and "probably unidentifiable with any population of *E. traillii* known at the present time" (Aldrich, *op. cit.*, p. 196). Considering the species as a whole, Brewster (1895) recognized a correlation between colour and geographic distribution. He included in the range of the nominate race all the region "south of the 42nd parallel of latitude" across the

continent and north to "Fort Resolution on Great Slave Lake, Fort Simpson on the Mackenzie River, Nulato on the upper Yukon, and British Columbia." He proposed the name *E. t. alnorum* for the population which "breeds in the Maritime Provinces, New England and New York, and Northern part of the Lower Peninsula of Michigan . . . and doubtless at many other points in the region lying immediately about the Great Lakes." This variant was described as, "coloring of the upper parts richer and more olivaceous."

Brewster's interpretation was accepted for a number of years until Oberholser (1918) studied the question and concluded that variation in the east did not sort out geographically, but he described a western segment in the south under the name *E. t. brewsteri*. The whole population east of the Rockies for a time thereafter was considered of the nominate race.

More recently Phillips (1948, pp. 509-510) proposed the recognition of a race, *E. traillii alascensis*, for Alaska, the Yukon, and northwest Mackenzie, largely on the basis of a longer wing and tail.

The most recent and exacting revision of *E. traillii* including eastern populations is that of Aldrich (*op. cit.*). He properly recognized the species as a late spring migrant and deleted specimens taken before June 21 from his comparisons. Thus the heterogeneity encountered by Oberholser (1918) for the east was eliminated.

A similar policy has been followed in the present study with slight modification of the dates used in eliminating migrants. Wanderers might be included during any period. Only those specimens collected between June 14 and August 7 were used for geographic comparisons; thus the series of approximately 340 specimens of eastern *Empidonax traillii* was reduced to 130. Specimens taken on earlier dates for more northern localities might have been used since they would be essentially in their geographic zone whether established for breeding or not, but the elimination of them has tended to equate the series used for comparison with respect to the condition of the plumage. None of the few August birds was from the south. The distribution of the critical specimens used in comparison is given at the end of this paper.

Preliminary comparisons of the 130 critical specimens indicated that there were average morphological differences between specimens from north of the Great Lakes and those to the south. Northern specimens were more olivaceous dorsally and

more yellow ventrally on the average. This was in general agreement with Brewster (*op. cit.*) and with Aldrich (*op. cit.*). In disagreement, no evidence supported the conclusion that the population centering in the south extends north through the Prairie Provinces of Canada to the far northwest. The boundary between the two populations, though still inadequately refined, especially in the west, extends from New York State westward through southern Ontario and Michigan to the prairies apparently approximating the international boundary in the west. A dozen of the 130 specimens originated from along this boundary. These were eliminated from statistical treatment.

Size: Specimens available have been inadequate to review the proposal of Phillips with respect to a longer winged, longer tailed Alaskan race. Three males from southern Yukon were measured as follows: Wing 73, 73.5 and 75.5 respectively; tail 60, 62 and 62.5. These measurements are not superior to those of a number of specimens originating from across Canada from Alberta to Quebec and certain specimens from more southern areas are not notably inferior to them in size. Comparisons of specimens from the two populations here recognized, i.e., northern and southern, show a tendency toward superior size in the north but this tendency was found not significant when the error of averages was calculated (table I; A, fig. 3). Although Phillips gave a maximum wing length (64.1) which is larger than any specimen examined in this study, such specimens could represent the ultimate in the trend toward larger size in the north which cannot be satisfactorily circumscribed geographically.

Colour: With respect to both the ventral and dorsal view, colour has been observed to have a broad geographic correlation. This was more apparent when the sexes were compared separately. Birds of the northern population usually display more "primrose yellow" ventrally, both in intensity and extent. Few northern specimens were notably white below. On the other hand, the majority of specimens from the south were whiter, less yellow ventrally, on the average. In order to convey the observations on colour of the ventral surface graphically, a standard series was established from the whole series, north and south, showing five grades from the least yellow to the most yellow. The steps in the standard series were slight and arbitrarily adjudged to be approximately equal. Every specimen in the whole series, north and south, was compared with the standard series and each was matched with one of the five

TABLE I. Comparative measurements of northern and southern populations of *E. traillii*. The number of measurements, in square brackets, is followed by the minimum and the maximum and the final figure, in parentheses, is the arithmetic average with its standard error.

	<i>Chord of Wing</i>	<i>Length of Tail</i>	<i>Exposed Culmen</i>	<i>Width of Culmen (at anterior nostril)</i>	<i>Total Length (collector's meas.)</i>	<i>Wing Spread (collector's meas.)</i>	<i>Tip of Secondaries to tip of primaries</i>	<i>Weight (grms.)</i>
Northern ♂♂	[67] 68.5-75.5 (72.7 ± .61)	[67] 54.0-62.5 (57.9 ± .22)	[66] 10.0-14.0 (11.2 ± .10)	[67] 4.5-6.1 (5.36 ± .04)	[27] 137-156 (147 ± .9)	[9] 220-235 (230 ± 1.8)	[67] 11.5-17.0 (14.1 ± .15)	[4] 12-14 (13.3 ± .50)
Southern ♂♂	[20] 68.2-74.5 (71.0 ± .35)	[20] 54.0-60.5 (56.8 ± .45)	[20] 10.0-13.8 (11.6 ± .12)	[20] 5.0-5.9 (5.42 ± .05)	[9] 136-149 (145 ± 1.9)	[2] 228-230 (229)	[20] 12.0-17.5 (14.2 ± .29)	[4] 12.6-15.0 (13.7 ± .59)
Northern ♀♀	[15] 65.0-71.0 (67.8 ± .42)	[15] 53.0-58.0 (55.0 ± .42)	[15] 10.0-12.0 (10.9 ± .21)	[15] 5.1-5.7 (5.4 ± .28)	[9] 136-149 (143 ± 1.6)	[6] 210-229 (216 ± 2.9)	[15] 10.0-15.5 (12.8 ± .27)	[4] 11.5-14.5 (13.0 ± .72)
Southern ♀♀	[16] 64.5-68.5 (66.8 ± .30)	[16] 53.0-58.0 (54.0 ± .39)	[16] 9.5-12.0 (10.9 ± .14)	[16] 4.7-5.8 (5.28 ± .73)	[4] 131-147 (139.2 ± 3.3)	[1] 214	[16] 10.5-17.0 (12.8 ± .50)	[1] 12.5

grades and scored accordingly. The sexes were treated separately. The most pronounced difference was displayed by males. Details of these comparisons are presented in table II. The yellowest specimens were from the grove belt of the Canadian prairies, particularly southern Manitoba.

Concerning the dorsal colour of the two populations, it was obvious that the northern population was more uniformly green on the back, "olive" being the most descriptive term for the series in general. Northern Michigan was the most southerly point where olive-backed specimens originated. In the south, specimens tend strongly toward "brownish olive," or the green is grayed considerably. Lake Nipigon, Ontario, was the most northerly point where brown-backed specimens originated. The brown and gray variation in the south presented a difficulty in comparing the southern with the northern group, but a standard series was again established to represent five barely perceptible grades, from the least green to the greenest in dorsal colouring. Whether a southern specimen was predominately brownish olive or grayed olive on the back, it scored low in the green scale. With this explanation of the difficulty and the probability of increased error, the results for both sexes are shown in table III.

These comparisons reveal a situation very like that originally described by Brewster (*op. cit.*) that birds from the north and east have the "upper parts richer and more olivaceous." Specimens with the brightest green backs were from the grove belt of the Canadian prairies, but the whole Canadian series, from the Rockies to the Maritimes, is remarkably alike in colour, dorsally. As stated above, the Canadian prairie specimens are unlike those representing the population south of the Great Lakes as suggested by Brewster (*op. cit.*) and Aldrich (*op. cit.*) The results of colour grading, both for the ventral and dorsal surface are graphically presented in fig. 3, B and C.

Tone: This feature was not found to be a satisfactory basis for segregating geographic populations. Differences are not sufficiently pronounced and variation is apparently local. The palest specimens examined during this study (excluding *extimus*) originated from Clay County, Iowa. The darkest are from the west coast of James Bay. The well distributed and recently collected series of specimens across the northern prairies in Canada is not appreciably paler in tone than the eastern Canadian series. There is a tendency to be purer in chroma and, as noticed under the remarks on colour, they belong with whole northern series on a colour basis.

One feature in which tone is involved concerns the contrast between the feathers on the cap and those of the back. In 90% of the northern birds the cap is the same tone (and colour) as the back, and in 10% the cap is slightly darker. In the southern series 40% were adjudged to have the cap and back the same tone (and colour) while 60% showed some darkening of the cap. This feature seems probably to result from feather wear and

TABLE II. Variability of amount of yellow, ventral view, northern and southern populations of *E. traillii*.

Grades	<i>Least Yellow</i> 1	2	3	4	<i>Most Yellow</i> 5	Mean Grade
Northern ♂♂		3	31	25	8	3.6 ± .09
Southern ♂♂	7	7	6			2.0 ± .18
						difference 1.6 ± .32
Northern ♀♀		4	9	2		2.9 ± .16
Southern ♀♀	6	5	5			1.9 ± .22
						difference 1.0 ± .23

TABLE III. Variability of amount of green, dorsal view, northern and southern populations of *E. traillii*.

Grades	<i>Least Green</i> 1	2	3	4	<i>Most Green</i> 5	Mean Grade
Northern ♂♂		2	18	37	10	3.8 ± .09
Southern ♂♂	10	6	4			1.7 ± .27
						difference 2.1 ± .22
Northern ♀♀		1	5	9		3.5 ± .18
Southern ♀♀	4	4	8			2.2 ± .22
						difference 1.3 ± .28

FIG. 3. Horizontal bar = arithmetic mean.

Vertical lines = two standard deviations above and below the mean.

Enclosed block = two standard errors above and below the mean.

A. Total length (collector's measurements) indicating the trend toward large size in northern *E. traillii*.

B. Grading of ventral yellow in eastern *E. traillii* 1 (least) to 5 (most).

C. Grading of dorsal green in eastern *E. traillii* 1 (least) to 5 (most).

degeneration in breeding birds, a change which seems to be more marked in southern populations of other species of birds as well.

Pattern: No plumage marking was found to be useful in distinguishing the two populations. The gray breast band is, on the average, a little more conspicuous on northern birds than on southern birds. This tends to produce a contrast with the throat thus imparting a whiter appearance to that area. (It is of interest to note that specimens from the Canadian prairies, which are richest in yellow, show this colour invading the gray breast band imparting to it a greenish cast in some specimens.)

Choice of ecological niche: Habitat in its entirety is difficult of

comparison on a geographic basis, but similarities or dissimilarities with respect to such elements as drainage can be compared. Considering first the region of the type locality of *E. traillii*, Arkansas, the writer is informed by Mr. Brooke Meanley who has recently studied the species there, that it occupies two habitat types, namely, "slashy" thickets bordering drainage areas, and islands of scrub vegetation (haw and persimmon) out on the prairie. Howell (1911, p. 54) states he had found it at Stuttgart, Arkansas, in orchards and door yards.

About the same diversity of habitat is indicated for Missouri by Widmann (1907, p. 142)—"along rivers, creeks and lakes, or clumps of willows in swampy places" and "in city parks and cemeteries, in orchards and the fringe of trees and shrubs along frequented country roads." Goss (1891, p. 369) refers to "groves and woods skirting streams and swampy land" for Kansas. Ridgway (1889, p. 356) mentions that the species often occupies situations in Illinois close to "dwellings, especially in orchards." Butler (1898, pp. 869–871) was undoubtedly making an ecological distinction in his treatment of the species for Indiana attributing one form to "open woods" and the other to "alder swamps and thickets."

At Buckeye Lake, Ohio, Trautman (1940, p. 295) states it "preferred" brush, 3 to 18 feet high, composed of such trees as small willows, alders, buttonbush and dogwood, with an occasional pair "in the more extensive cat-tail marshes." As a minority choice he states that a "few nested in the drier, brushy fields such as was the favoured habitat of the Field Sparrow."

The dryland habitat in Ohio has been particularly well stressed by Campbell (1936) whose description is accompanied by a photograph. Almost precisely the same type of situation was found to be occupied by *E. traillii* by Mr. J. L. Baillie on Pelee Island, Ontario, in 1950. It is perhaps particularly noteworthy that the Pelee Island colonies are only 50 miles from the Lucas County, Ohio, colony described by Campbell (*op. cit.*). Mr. Baillie's field data reveal that the Pelee Island birds occupied dry pastureland where the prominent vegetation consisted of scattered clumps of cockspur hawthorn, fragrant sumac, and red cedar and that the terrain was dry with limestone outcropping through thin soil.

Schorger (1929, p. 3) states concerning Dane County, Wisconsin that *E. traillii* "is found in two types of cover: clumps of dogwood, low willows, etc., in marshes; and in large areas of sumac on the uplands."

Although the species appears to choose a dry habitat in southern settled regions more frequently than in the north, a corresponding variation does occur in northern regions. With respect to Maine in the northeast, Palmer (1947, p. 355) states "I associate the species mainly with abandoned damp fields or cut-over woodlots that are growing up to alder, the clumps of which are small and somewhat scattered, rather than dense and mature Dry fields having clumps of deciduous bushes also are favored places in summer."

Godfrey (1949, p. 24) found the species in the Mistassini region of Quebec "in the alder-willow margins of the lakes, in alder bogs and alder openings in the forest, and occasionally . . . in alder-birch-aspen second growth on higher ground."

For Ontario, north of Pelee Island, and south of the evergreen forest, the species is most apt to be established in the alder, scrub willow, arbor vitae fringes of creeks. It is not known by the writer to inhabit town shade trees, cemeteries, orchards, and other similar dry situations. Northward and westward in the evergreen forest region of the province it is most commonly found in wet alder and willow swales, but occasionally it is established in stands of young aspen poplar (four to ten feet high) in dry terrain.

Mr. T. M. Shortt informs the writer that in eastern and northern Manitoba, *E. traillii* occurs most frequently in wet scrub willow swales, but in the grove belt of the prairie it occupies the "bluffs" of young aspen poplar. For the most part, willow and alder swales seem to predominate as a habitat for the species in the northern prairies (Fleming, 1920, p. 403; Houston, 1949, p. 232). Some divergence was noticed by Mr. Dewey Soper who states (MS) that in Prince Albert National Park, Saskatchewan, the species is occasionally found in small tracts of black spruce muskeg. Farley (1932, p. 43) includes young poplar (dryland) as a habitat of the species for the Battle River region, Alberta.

The foregoing shows no marked difference with respect to choice of ecological niche between the northern and southern population insofar as drainage is concerned. Both populations show a wide tolerance, with the frequency of occupancy of dry areas possibly being somewhat higher in the south.

Song: Variability of song in *E. traillii*, not merely variation in ornithologists' onomatopoeic recording, is indicated by the literature. The first author to suggest a geographic correlation is Peterson (1939, pp. 99-100) whose remarks were based on

personal experience. To compare the song descriptions of authors is fraught with difficulty but has some merit. McCabe (1951) has recently undertaken to classify the song records of authors, and to be critical of his classification rightly subjects one to similar criticism. However, a few amendments are attempted in connection with McCabe's classification to which the reader is referred. (Since the above was written, a note has been published by Allen (1952) on this subject.)

Throughout Ontario, except in the extreme south, *E. traillii* sings a dry, somewhat burred and husky 'zweebeco', the accent falling on the second syllable, 'bee', and in effect the whole is declarative, i.e., the voice falls slightly with the 'o'. This song is shortened commonly, possibly by the same individuals, to 'zweebec', with slight accent on the second syllable and the general effect is interrogative, i.e., the voice is raised slightly with 'bee'. The sound has good carrying power. I do not hesitate to classify this song, in either the three or two syllable form, under McCabe's 'phe-be-o' or "eastern" group. The 'phe-be-o' song is the one heard throughout most of Canada and it has been variously recorded such as, "we're here" by Taverner (1934, p. 292) and "right here" by Farley (*op. cit.*, 42). There are many other onomatopoeic coinages of this song by authors, but a particularly apt one with definite geographic connotation is that of Allen (1902, p. 85) who records it as 'wee-zee-up', for Maine, New Hampshire, Vermont, Massachusetts, and Nova Scotia. The reader is referred to the commercially available folio of phonograph records ("American Bird Songs," record 1, side B, produced by the Albert R. Brand Song Foundation, Lab. of Ornith. Cornell Univ., Ithaca, New York) for a sound recording of this song taken at Bay Pond, western Adirondacks (information on the locality communicated to the writer by Mr. Kenneth C. Parkes who states that this is the song one hears in both the Adirondacks and the Catskills of New York).

With reference to McCabe's classification, I suggest that the following renderings of authors should be classified with the 'phe-be-o' or "eastern" (and northern) group—'Greadeal', 'Greadeal', (both Massachusetts) 'Re-peal' (New York) and probably 'Tick-weeah' (New York). No less an authority on field observation than Griscom (*loc. cit.*) uses 'phe-be-o' and 'great de-al' synonymously for the New York City region and states that the accent is always on the middle syllable. Remembering the shortened two-syllabled phase of this song (zwee-bee) would seem to admit 'Qui-dee' (New York) and 'Raiz-wee' (Massa-

chusetts) to this group also. Two other suggestions concerning McCabe's classification may be made. The '*Eaze-we-up*' (of Howell) is probably erroneously attributed to Florida and Alabama since the species does not breed in either state and probably does not sing there. One can therefore assume that Howells' song version has no geographical significance. Further, the '*Che-bee-u*' (of Nice) attributed to Oklahoma was not based on personal experience with the species in the field, according to Mrs. Margaret Nice (letter). Thus the '*phe-be-o*' song is geographically distributed through the northeast and across Canada.

What must be regarded as a different form of song, one apparently not heard north of about latitude 43° in southern Ontario, has been notated by Mr. George North (pers. commun.). Mr. North states that in the Hamilton region the '*phe-be-o*' song is sometimes alternated with a song he records as '*itty-peer*', the accent falling on the '*peer*'. The rendering most similar to this interpretation for an eastern *E. traillii* is that of Sutton (1928, p. 91), '*becky-weer*', for Pennsylvania. Another apparently irregular song is that of Trautman (*op. cit.*, p. 296) who describes the song at Buckeye Lake, Ohio, as a "slowly drawled *sweet-cheeuu*." However, McCabe (*op. cit.*, p. 91) has a satisfactory explanation of this on the basis of an introductory note sometimes introducing the '*fitz-bew*' song discussed later. There is also some uncertainty with respect to the song elsewhere in Ohio. Campbell (*op. cit.*, p. 168) states that in Waterville Township, Lucas County, Ohio, the '*whis-key*' call (which might be interpreted as the song next to be described) was given much less frequently than normal and instead, the song sounded much more like '*whee-bee*' or rarely '*whip-wheu-whip*'. The '*whee-bee*' is reminiscent of the two syllabled northern song. Campbell's '*whip-wheu-whip*' suggests an alarm call.

The two colonies of *Empidonax* on Pelee Island sing a song very different from that heard across Canada and in New England. The song has been heard by several ornithological colleagues with auditory acumen. Mr. James L. Baillie has described it to the writer as an abrupt, explosive sneeze, seemingly higher in pitch and less husky than the song heard in northern Ontario, the accent falling on the first syllable, '*witziu*'. The carrying power was not great. Obviously this belongs with the '*fitz-bew*' mid-western song of McCabe's classification, the song which Peterson (*op. cit.*) originally attributed to Ohio, and to western New York (specimen data). The writer is informed that Dr. Allen W. Stokes, who is familiar with the song of

E. traillii in southern Wisconsin and is also acquainted with the Pelee Island colonies, finds no difference between the songs heard in these regions. This song, or slight variations thereof, has been rendered 'pit-too' by Gibbs (1898) for (southern) Michigan; Gibbs was particularly adept in such particulars as will be evident from a perusal of his article. Mr. Brooke Meanley interprets this song as heard in Arkansas (pers. commun.) as 'witch-ew' or 'witch-ow'. Goss (*loc. cit.*) uses the phonetic 'Kewick' for Kansas.

Admitting certain difficulties, the writer submits that there are two distinct types of regular song of *E. traillii* east of the Rockies and that each has a broad geographic correlation. One belongs to the northeastern United States (Adirondacks, New England) and across Canada; the other from the Great Plains and the Mississippi drainage eastward south of the Great Lakes to New York. Irregularities and confusion seem most apparent in Wisconsin (McCabe (*op. cit.*, p. 95) states that 're-peal' and 'grea-deal' are sung there in addition to 'fitz-bew' with variations), southern Ontario (see North above), and Ohio (Trautman, *op. cit.*; Campbell, *op. cit.*). The matter seems to be clarified if we regard these localities as borderline between two intergrading or intermingling entities.

Nest: The nest of *E. traillii* is characteristically situated in the upright fork of a shrub or small tree; sometimes on a horizontal support (Fargo, 1928, p. 219). Two types of nests are built by the species and apparently there is a geographic correlation in this connection. Throughout Ontario (with the probable exception of Pelee Island and extreme southern counties) the nest is made of long, relatively coarse materials and though compact internally it displays straw streamers from the sides and bottom. This sparrow-like type of nest is common to Canada east of the Rockies and may be found south at least to Minnesota (Roberts, 1932, p. 20, fig. 308) and to New York (Eaton, 1914, illust., p. 198). From New York westward in the prairie extension region south of the Great Lakes and south to the limit of breeding range, the nest is a compact cup, as illustrated by Bent (*op. cit.*, pl. 25), composed of fine fibres, often including gray materials. This type of nest somewhat resembles that of *E. minimus* (see Bent, *op. cit.*, pl. 28) but is even more similar to that of *Dendroica petechia*. This is the type of nest either figured or described by the following authors: Bent (pl. 25) for Buffalo, New York; Campbell (*op. cit.*, 167, figs. 31 and 32) for northeastern Ohio; Trautman (*op. cit.*, 295) for east central

Ohio; Schorger (*op. cit.*, p. 3) for southern Wisconsin; Butler (*op. cit.*, 870) for Indiana; Mr. Brooke Meanley (MS) for Arkansas; and Goss (*op. cit.*, 370) for Kansas. There seems to be no reasonable basis for supposing that these two structural and architectural types of nest result from such a factor as availability of material. Though long, coarse straws may predetermine an untidy nest, surely this material is universally available. The two types seem to be an expression of some physiological differences in the two populations. There is the possibility that nests intermediate in appearance may be found in geographically borderline areas.*

Other differences: Comparative field studies concerned with other possible differences may well receive attention. Observations, not discussed above, suggest that *E. traillii* in the north is more inclined to skulk; those in the south tending to seek more exposed and higher perches. Also, it is suggested that southern birds are inclined to perch in a more upright position.

Discussion: The foregoing indicates that there are two separable populations of *E. traillii* east of the Rocky Mountains. Morphologically there is but a slight, average difference. The population occupying the area from the northeastern United States across Canada to Alaska (fig. 4) is more constant in the display of both the morphological and non-morphological characters attributed to it. It is characterized by a comparatively greener (olive) dorsal surface and more yellow pigment on the ventral surface, the sexes compared separately. Those brightest in colour occur in Manitoba and those darkest in tone originate in the James Bay region. The slight tendency toward a larger size is not a significant and useful character on which recognition of this race can be based, though the largest occur in the far northwest. The song common to this population is distinct from that of the southern populations, any confusion apparently being limited to borderline regions. Its form is represented by the phonetics, 'zwee-beeo', or 'wee-zee-up' or 'phe-be-o', etc., some-

*Since this was written, a nest and descriptive details received from Dr. W. W. Judd have been found to fit the idea of intermediacy. The nest was found near London, Middlesex County, in extreme southern Ontario. It was built five feet from the ground in the crotch of an elder (*Sambucus*) surrounded by cat-tails. It is constructed of fine gray plant fibres (like southern *E. traillii*) but is loosely woven outside and has six-inch streamers of material from the bottom (like northern *E. traillii*). The bird concerned had a grayish back and head, and white underparts slightly gray on the chest (like southern *E. traillii*). Its song was of three syllables, rendered by Dr. Judd as 'pu-pwee-oo' with the accent on the second syllable (like northern *E. traillii*).

FIG. 4. Distribution of characters of eastern *E. trailii*.

Vertical lines cover the area where the species is characteristically olive dorsally and the majority of specimens are relatively yellow ventrally; the song is represented by 'zweebeco' or 'eaze-we-up'; the nest is sparrow-like with bottom streamers of straw.

Vertical dashes cover the area where colour is somewhat intermediate or all colour characters may occur and where the song and nest are apparently most variable.

Heavy lines bound the range of the species which is usually brownish olive dorsally, sometimes grayish olive, and where the majority of specimens are relatively white ventrally; the song is represented by 'witziu' or 'fitz-bew'; the nest is felted and yellow warbler-like.

Heavy dashes bound the area where material examined is inadequate but available evidence suggests a continuation of the heavy lines.

times shortened to 'zweebeco'. The accent in either the three or two syllable song is on the second syllable. The nest, an untidy structure of straw and plant stocks, is peculiar. The race seems to prefer wet thickets but will also invade dry habitats of an edge nature.

The southern population, which ranges from the great plains of the United States eastward in the prairie extension (Schmidt, 1938) to New York (fig. 4), averages less green on the back, which area displays more variation in actual colour—many specimens being brownish olive, and some tend to be grayed olive (Pelee Island, Ont., etc.). Specimens from the western plains are somewhat paler in tone, but the collection studied does not indicate an adequate basis for further taxonomic separation. Ventrally the southern population is whiter below, i.e., less yellow, on the average. The song of this population, though possibly somewhat variable, is unlike the song of the northern race. The form of the song is represented by, 'witziu', or 'pit-too', or 'fitz-bew', etc., the accent falling on the first syllable. The nest is a felted structure including gray plant fibres and has the general appearance of that of the yellow warbler. It is quite unlike the nest of the northern race, though it seems to resemble that of *E. t. brewsteri* (Dawson, 1923, p. 884). On the basis of the literature this race apparently is more frequently inclined to occupy dry habitat including the environs of human habitations than the northern race.

It will be recognized that the characters on which the two eastern populations of *E. traillii* are distinguished are essentially of the same nature as those used in identifying eastern species of *Empidonax*. Morphological differences are slight and largely a matter of degree. There is convincing evidence of a constant difference with respect to type of nest, and strong evidence that the songs of the two populations are distinctive. Such non-morphological characteristics have been shown to be of particular importance in discriminating between species in this genus. In this light one might consider that these forms of eastern *E. traillii* closely approach the threshold of specific difference. However, they can be treated only as geographic races, differentiated on slight and average morphological characters. Taxonomically, the identity of individual specimens is often uncertain.

With respect to nomenclature, the writer cannot confirm Aldrich's belief (1951) that the population in the middle south, i.e., south of the Great Lakes and to Arkansas, need be provided with a new name (*E. t. campestris*). Without access to Audubon's type, I have Aldrich's statement (p. 193) that the specimen "is an example of the dark greenish northern and eastern boreal population." He further states (p. 194) "although the sex is not indicated on the label, [it] is almost certainly not a female, but

a male, and a big one at that, with a wing of 74 mm. (larger than the maximum for females of even the Alaskan population).'' In describing the prairie race (including the population south of the Great Lakes) Aldrich's type series of males (12 breeding specimens from North and South Dakota) shows a range in chord of wing from 69 to 75 mm., a maximum greater than Audubon's type, thus demonstrating that Audubon's type could belong to the southern population on the basis of size. The writer has measured a male from Monroe County (southeastern) Michigan, taken on July 8, which had a wing 74.5 mm. in length. Size is therefore not helpful in deducing the probable breeding zone of Audubon's type. The matter must rest on colour and tone. This study indicates that tone is not a useful characteristic in distinguishing populations east of the Rockies. Colour has been found useful, applied to populations, but it is not an infallible guide applied to individuals. One can only conclude that the identification of Audubon's type is not beyond doubt. It appeals to the writer as most reasonable to retain the name *E. t. traillii* (Audubon) for the southern population, in view of the uncertainty pertaining to the type and the long established connotation of the trinomial, and that *E. t. alnorum* Brewster be applied to northern birds across Canada from the north-eastern United States to Alaska, including the Canadian prairies.

DISTRIBUTION OF CRITICAL SPECIMENS OF *E. traillii*
COLLECTED BETWEEN JUNE 14 AND AUGUST 7

Yukon, southern 3; *Alberta*, northern 3, central 8, southern 4; *Saskatchewan*, central 6, southern 1; *Manitoba*, northern 1, central 1, southern 9; *Ontario*, northern 15, western 4, central 12, southern 14; *Quebec*, central 12; *New Brunswick*, 1; *North Dakota*, southeastern 1; *Michigan*, northern 6; southern 12; *Colorado*, eastern 1; *Iowa*, northern 4; *Ohio*, northern 10, southern 2. Total 130 (including 12 from southern Ontario and northern Michigan, representing an intermediate zone, which were omitted from the statistical comparisons).

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