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COMMENTS ON THE TAXONOMY OF
EMPIDONAX TRAILLII (WILLOW FLYCATCHER)

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Traill's Flycatcher (sensu American Ornithologists' Union [A.O.U.] 1957) is now recognized (A.O.U. 1973) as two species, *Empidonax traillii* (Audubon, 1828) (Willow Flycatcher) and *E. alnorum* Brewster, 1895 (Alder Flycatcher). The two species do not interbreed (Stein 1958, 1963, Gorski 1970), differ genetically (Zink and Johnson 1984, Seutin and Simon 1988), are usually though not always separated ecologically (Stein 1958, 1963, Barlow and McGillivray 1983, Zink and Fall 1981, Ewert 1981), and differ in song and calls (Stein 1958, LeGrand 1979, Lehman 1985). *Empidonax traillii* vocalizes the "fitz-bew" song and breeds in swamps and willow thickets, usually along streams, in the conterminous United States and southern Canada. *Empidonax alnorum* vocalizes the "fee-bee-o" song and breeds in shrubs and alder thickets of the northeastern United States, Canada, and Alaska.

Empidonax traillii and *E. alnorum* are similar in size and proportions (Russell 1990, Seutin 1991). Although some specimens and birds in the hand may be identified to species by means of Stein's (1963) formula (Phillips et al. 1966, Pyle et al. 1987), the reliability of the formula was questioned by Seutin (1991). The back in *E. traillii* is dull and gray or brownish olive whereas in *E. alnorum* it is usually a brighter greenish (Phillips et al. 1966).

Eugene Eisenmann discussed the reasons for assigning the specific name *traillii* to the Willow Flycatcher in a paper he read at the A.O.U. meeting in 1969 (fide Bull 1974). The only more recent comments on the status of the name are brief statements by Eisenmann (1970:108) that "Audubon's name *traillii* belongs to the Arkansas prairie population, which is a 'fitz-bew' vocalizer" and by the A.O.U. (1973) that Audubon's (1828, 1831) description of *traillii* was based on unpreserved specimens of an apparently mated pair. Details to support these conclusions were never published. Because the status of Audubon's birds and therefore the application of the name *traillii* have been questioned (e.g., Aldrich 1951, James and Neal 1986), I discuss these issues here in more detail.

I also discuss the taxonomic status of *E. t. campestris*, a name synonymized with nominate *traillii* by Unitt (1987). Because I agree with most of Unitt's conclusions about the western populations, my comments on those birds are limited mostly to reported zones of intergradation between the western subspecies.

APPLICATION OF THE NAME TRAILLII

The Identity of Audubon's Birds

Audubon (1831) obtained two flycatchers from the "woods along prairie lands of Arkansas" (= Arkansas Post, about 42 miles southeast of Pine Bluff, in Arkansas County, southeastern Arkansas) in April 1822. The Western Birds 24:241-257, 1993

original painting of the flycatcher was inscribed "Fort of Arkansas April 17, 1822" (Durant and Harwood 1980: 198), three days before Audubon returned to Natchez, Mississippi (Arthur 1937). Audubon (1831) reported that the female contained five eggs about the size of green peas, and he suspected, but did not find, a nest. He also reported that the length of the birds was 5 $\frac{3}{4}$ inches and their flight call as "wheel, wheel."

The bird illustrated by Audubon (1828) has wing-bars and an eye-ring typical of *Empidonax*. Five species of *Empidonax* occur in Arkansas (James and Neal 1986): *flaviventris*, *virescens*, *minimus*, *alnorum*, and *traillii*. Compared with Audubon's illustration, *flaviventris* and *virescens* are greener above and more yellow below, and *minimus* is grayer above. The bird illustrated is similar in color to both *alnorum* and *traillii*. James and Neal (1986) listed *alnorum* as a transient infrequently reported in spring and very rarely in fall, and *traillii* as a migrant and now becoming extirpated as a breeding bird. The flight call of "wheel, wheel" (Audubon 1831) resembles the "whit" call (Stein 1963) of birds that sing the "fitz-bew" song. Although the "whit" call is given during migration (Lehman 1985), the call is also given in response to an intruder near a nest (Stein 1963). Even though calls by other species in *Empidonax* might be rendered "wheel" or "whit" (J. P. Hubbard in litt.), most authors (e.g., Lehman 1985) usually equate "whit" with *E. traillii*.

The earliest arrival of *E. traillii* in Arkansas is early May (James and Neal 1986), and the earliest paired birds are on their territory is 10 May (Meanley 1952). Aldrich (1951) believed that the date 17 April of Audubon's birds was too early for breeding. However, April sight records of the species at other localities suggest that breeding of *E. traillii* could occur earlier than normal (mid-May to June). Willow Flycatchers have arrived north of Arkansas as early as 24 April in Indiana (Mumford and Keller 1984) and 18 April in Ohio (Peterjohn 1989). The earliest arrival in Oklahoma, just west of Arkansas, is 20 April (Sutton 1967). An early arrival date of 21 April has been reported from western Oregon (Gabrielson and Jewett 1940), of 29 April from eastern Oregon (Littlefield 1990a). Oberholser (1918) reported a specimen (U.S. National Museum (USNM) 109499) collected 8 April 1885 at San Angelo, Tom Green County, central Texas. Although identified as *E. t. campestris* by Aldrich and as *E. t. adastus* by A. R. Phillips, neither author mentioned the specimen in his publications on *E. traillii*. Males arrive on their breeding grounds, on an average, earlier than females (Jussell 1991), and pair formation occurs on the breeding grounds (Holcomb 1974). It is implausible that a female would be migrating with a full clutch of developing eggs.

Because Audubon's (1828) illustration can be identified with either *E. alnorum* or *E. traillii*, and because the female must have been on the breeding grounds, several conclusions about the identity of Audubon's birds are possible: the birds are Alder Flycatchers because the breeding range of *alnorum* 165 years ago extended to Arkansas; a pair of *E. alnorum* bred unusually far south of the species' present breeding range; the two birds are an unknown species; Audubon fabricated the dates and/or the reproductive condition of the female; the birds are *E. traillii* that arrived and bred earlier than the average for the species. Although any one of these conclusions is

possible, only the last is reasonable. Because the holotype of *traillii* is lost (see below), it is not possible to prove that Audubon's birds were Willow Flycatchers. However, *E. traillii* is the only species that resembles Audubon's illustration and breeds in Arkansas. I conclude that nomenclatural stability is best served by retaining the name *traillii* Audubon as the specific name for the Willow Flycatcher.

Audubon's (1828) illustration is of a bird darker above than *E. t. adastus* and *extimus* from western North America and *E. t. campestris* from the northeastern and north-central United States. Compared with *E. t. brewsteri* from west of the Cascade Range and Sierra Nevada, the back and head are more concolorous; in *brewsteri* the top of the head is darker than the back. Audubon's birds are identifiable with the population of *E. traillii* that breeds in the southeastern range of the species (Brewster 1895, Phillips 1948).

The Alleged Lectotype of *Empidonax traillii*

Ridgway (in Brewster 1895) labeled as types three specimens (USNM) of *E. traillii* that Spencer I. Baird had received from Audubon. Oberholser (1918) reidentified two of the specimens as belonging to the Columbia River population (*E. t. brewsteri*); Audubon (1839) listed that locality and may have received specimens from there collected by John K. Townsend or Thomas Nuttall (Graustein 1967). Oberholser (1918) concluded that the third specimen, USNM 1865, was collected by Audubon on the Arkansas River and belongs to the eastern subspecies. Neither Ridgway nor Oberholser actually designated (International Commission on Zoological Nomenclature [ICZN] 1985, Art. 74) USNM 1865, or any other specimen, as a type or lectotype of *traillii*. Phillips (1948), however, did formally designate USNM 1865 as the lectotype of *Muscicapa traillii* Audubon and it was referred to by Aldrich (1951) and Deignan (1961) as the type specimen of the Willow Flycatcher. (A lectotype is a single name-bearing type specimen designated subsequent to the original description; lectotypes are designated from specimens of a type series that are called syntypes.)

Aldrich (1951) identified USNM 1865 as a migrant resembling longer-winged and darker populations from Alaska (now *E. alnorum*); he believed that the breeding population of central-eastern Arkansas belonged to the paler subspecies *E. t. campestris*. Two of the specimens he examined are from near Stuttgart, Arkansas (about 35 miles northwest of Arkansas Post), an area ecologically distinct from the type locality of *traillii* (G. Graves pers. comm.). The two specimens are intermediate between nominate *traillii* and *campestris* (see beyond for taxonomic comments on *campestris*). Snyder (1953:23) pointed out that the wing chord of USNM 1865 is in the size range of *campestris* and concluded that its identification "is not beyond doubt."

The subspecific identity of USNM 1865 is nomenclaturally important only if the specimen can be associated with Audubon and his description of *E. traillii*. According to Eugene Eisenmann (in a letter to J. W. Aldrich, 20 January 1969, U.S. Fish and Wildlife Service files, Division of Birds, Smithsonian Institution), Audubon was unaware of the importance of

preserving specimens in 1822 and possibly did not begin to preserve birds until sometime in 1830. Eisenman based his suggestion on Audubon's not mentioning preserved specimens in his journals and his receiving in 1830 from Swainson a letter that contained passages (see Deane 1905) on the importance of preserving specimens. But Audubon had at least been exposed to the idea of preserving specimens by 1820 when he was a taxidermist at Cincinnati (Ford 1988), and had met Filian Peale and Thomas Say, who preserved specimens on the Long Expedition of 1819-1820 (Brodhead 1978). There is no evidence, however, to indicate when Audubon began preserving specimens.

Even if Audubon preserved specimens of *E. trailii* from Arkansas in 1822, no collection data can be associated with USNM 1865. Measurements of the specimen do not conform with those given by Audubon (1831). Furthermore, because of the specimen's worn plumage, it is highly probable that USNM 1865 was not collected in April. Willow Flycatchers molt in their winter range and are in fairly fresh plumage when they arrive in the United States (Unit 1987). Thus USNM 1865 was not from a type series and therefore does not fulfill the requirements for a lectotype (see ICZN 1985, Article 74). Because Audubon's Arkansas birds are apparently lost, and may never have been preserved, the plate itself offers the only evidence of the subspecific identity of the population. The bird illustrated (Audubon 1828) must stand as a lectotype of *E. t. trailii*.

SUBSPECIES OF *EMPIDONAX TRAILLII*

Taxonomic History

Traylor (1979) stated that the subspecific taxonomy of *E. trailii* cannot be worked out without long series of fresh specimens of known song type. Although perhaps it was not his intent, Traylor implied that because the original descriptions of subspecies of *E. trailii* did not include information on song and thus specific identity, each of the subspecific names could be construed as being a *nomen dubium* (i.e., name of unknown or doubtful application).

The type locality of *E. t. campestris* (Oakes, Dickey County, North Dakota) is within the breeding range of the species *E. trailii* (Stewart 1975) but is near localities where C. T. Clark (in litt.) reported *E. alnorum* singing and calling. After examining the holotype of *campestris* (USNM 259504), I conclude that its plumage and measurements (e.g., Stein 1963, Pyle et al. 1987) agree with those of the species *E. trailii* rather than with those of *E. alnorum*. The holotypes of four named subspecies of *E. trailii* from west of the Rocky Mountains were collected hundreds of miles from the nearest breeding populations and migration routes of *E. alnorum*. The eight records of the Alder Flycatcher near the type locality of *E. t. adastus*, of a single bird in northeastern Oregon (Roberson 1980) and a small population breeding (songs recorded) at Malheur National Wildlife Refuge, southeastern Oregon (Whitney and Kaufman 1986), are likely erroneous. The Oregon Bird Records Committee rejected the northeastern record because the documentation was insufficient to support the identification (Watson

1981), accepted the two Malheur reports (Watson 1984, Irons and Watson 1985), and did not mention breeding. However, J. A. Sedgwick and C. D. Littlefield (pers. comm.), both of whom have spent considerable time working at the refuge (Sedgwick and Knopf 1989, Littlefield 1990a, b) doubt the authenticity of these records.

Regardless of the possible occurrence of other species of *Empidonax* at their localities, the holotypes of the subspecies of *E. trailii* are morphologically identifiable as Willow Flycatchers and represent breeding populations that sing the typical song of *E. trailii* (e.g., King 1955, Green 1978, Phillips et al. 1964, pers. obs.). Nomenclatural stability is best served by regarding the names of subspecies of *E. trailii* as representing that species.

Brewster (1895) proposed the name *Empidonax trailii alnorum* for a subspecies that breeds in the Maritime provinces of Canada, New England, New York, and Michigan. He gave the breeding range of nominate *trailii* as from central Alaska to British Columbia, western United States west of the Great Plains, and the southern Mississippi Valley, including Arkansas. Brewster (1895) characterized *alnorum* as more olivaceous above than nominate *trailii*. Oberholser (1918) concluded that northeastern populations and those from Arkansas were not distinct from one another, synonymized the name *alnorum* with nominate *trailii*, and proposed the name *brewsteri* (type locality Cloverdale, Nye County, Nevada) for the Willow Flycatchers breeding from southwestern British Columbia and much of the western United States east to eastern Oklahoma and northeastern Texas. He characterized *brewsteri* as more brownish above than *trailii*. He did not include eastern Oregon in the range of *brewsteri*, and later (Oberholser 1932) proposed the name *adastus* (type locality Hart Mountain, northern end of Warner Valley, 20 miles northeast of Adel, Oregon) for a subspecies that breeds from eastern Washington and Oregon to northeastern California, Idaho, northern Nevada, Wyoming, western Montana, and central Colorado. He referred to birds from northern Utah, central Colorado, and north-central California as intergrades between *brewsteri* and *adastus*. Oberholser (1947) named as *zopholegus* (type locality "South Vancouver Island," British Columbia) the subspecies breeding from southwestern British Columbia to western Washington, Oregon, and Marin County, California. He characterized *zopholegus* as smaller, darker, and browner (above) than *adastus*; he did not contrast *zopholegus* with *brewsteri*.

Phillips (1948) recognized nominate *trailii*, with *alnorum* as a synonym, and synonymized *zopholegus* with *brewsteri* (its type specimen being a migrant "*zopholegus*"), and recognized *adastus*. He also proposed the subspecific name *extimus* (type locality lower San Pedro River, Arizona) for a pale subspecies of *E. trailii* breeding from southern Nevada to southwestern Utah, central and central-eastern Arizona, southwestern New Mexico, and western Texas. Aldrich (1951) recognized the same western subspecies as Phillips (1948) and proposed the name *campestris* for the pale greenish populations that breed from Mackenzie to the Great Plains and east to western New York. Specimens from Mackenzie and all but the southern portions of the Canadian prairie provinces that Aldrich (1951) identified as *campestris* represent allopatric populations of *E. alnorum* (see Godfrey 1986). The A.O.U. (1957) included *adastus* and *extimus* in the subspecies

brewsteri and included most of the range of *campestris* in nominate *trillii*.

Unitt's (1987) taxonomic assessment of *E. trillii* resembles that of others (e.g., Phillips 1948, Aldrich 1951, Wetmore 1972) for the western subspecies, with the exception of extending the breeding range of *extimus* to Baja California and southern California and including in *adastus* birds from the purported (Burleigh 1972, Behle 1985) zones of intergradation between *extimus* and *adastus*. He synonymized the name of the midwestern subspecies *campestris* with nominate *trillii* (contra Sutton 1967 and others). However, Unitt's (1987: tables 1 and 2) series of nominate *trillii*, according to the localities he reported, were from the range of *campestris* rather than from the range of nominate *trillii* (sensu Aldrich 1951).

Methods

To reevaluate the taxonomic status of *campestris* and the other subspecies, I examined 270 adult breeding specimens of *E. trillii* and the holotypes of *brewsteri* and *campestris*. I had earlier (Browning 1979) examined the holotype of *adastus*. Specimens collected north of about 37°N latitude in June and July I considered to have been on their breeding grounds. Durations of migration and breeding overlap, especially south of 37°N (see Phillips et al. 1964, Unitt 1987). Examples of breeding durations (nest building to fledging) north of 37°N are late May to mid-July in Washington (Jewett et al. 1953), June to mid-July in eastern Oregon (Littlefield 1990a), early June to mid-July in Idaho (Burleigh 1972), June to late July in North Dakota (Stewart 1975), early June to mid-July in Indiana (Mumford et al. 1984), and mid-June to mid-July in Ohio (Peterjohn 1989). Egg dates in Ontario extend from 13 June to 20 July (James 1991). Because the identifications of *adastus* and *brewsteri* are well established by others (e.g., Phillips 1948, Aldrich 1951, Unitt 1987), with whom I agree, I considered dark-backed specimens from the southwestern parts of the breeding range of *E. trillii* as migrants. In order to exclude potential migrants, specimens from regions of alleged intergradation between subspecies and those used for determining the taxonomic status and ranges of *campestris* and nominate *trillii* were collected from mid-June to mid-July unless otherwise stated. I compared both old and new specimens, bearing in mind that geographically similar samples collected in the last three decades average slightly darker and greener (less brownish) than those collected earlier. Specimens with heavily worn or foxed plumages were not included in the study.

Evaluation of plumage colors by Smithe's (1975) color standard was not possible because his color swatches generally do not match actual colors (Pratt and O'Neill 1976) and specifically do not match plumage colors of Willow Flycatchers (Unitt 1987). Furthermore, the criteria that a color standard should have the same texture, gloss, and colorants (dyes, pigments) as that being compared (Hale 1987), are not met when color swatches are compared with birds. Although Munsell Color Charts (1990) present many of the same problems, I used Munsell's standards to deter-

mine relative values (pale vs. dark) for the crown and backs of most specimens (Figure 1). Value for other specimens was determined visually by direct comparisons of specimens. Analysis of measurements (e.g., wing chord, tail, bill) revealed no taxonomically important differences in size between populations. Because Stein's (1963) wing formula for identifying *E. trillii* and *E. alnorum* is not reliable for all specimens (Seutin 1991), I excluded specimens of *E. alnorum* from the sample of *E. trillii* by using a combination of plumage color and pattern discussed under *E. t. trillii* (below).

Results

Comparison of specimens revealed that there are five recognizable subspecies of *E. trillii*. Nominate *trillii* is similar in plumage to *E. alnorum* (see below); other subspecies (*brewsteri*, *adastus*, *extimus*, and *campestris*) are much browner and less greenish than Alder Flycatchers.

Empidonax t. trillii. Unworn specimens of *E. alnorum* are usually brighter green (less brownish) on the back and crown than specimens of *E. trillii*. The crown feathers of *alnorum* usually have brownish centers, whereas these feathers in nominate *trillii* are usually more solid in color.

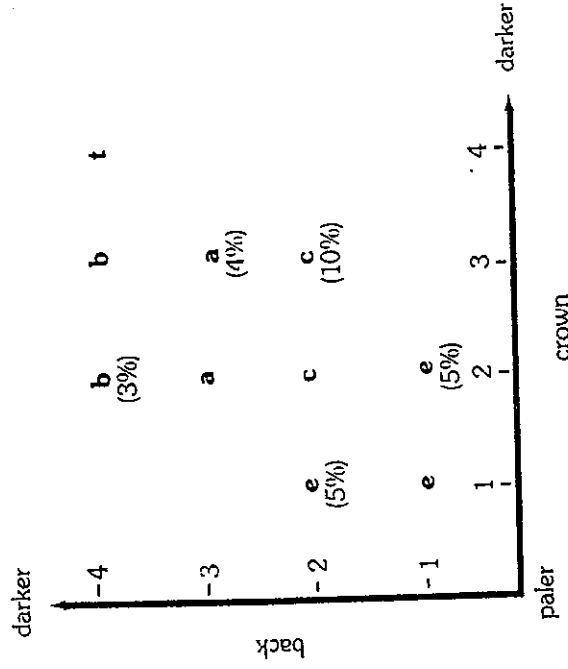


Figure 1. Relative values of back and crown color of unworn adult *Empidonax trillii*. Letters represent 100% of a sample, unless otherwise indicated, as follows: t, nominate *trillii* (sample size, 11); c, *campestris* (20); b, *brewsteri* (62); a, *adastus* (125); e, *extimus* (18).

These differences, as with Stein's (1963) wing formula, are not 100% reliable.

The nominate subspecies is darker and less greenish (more brownish) on the back and crown than *campestris*. Although *trairllii* and *campestris* each have similar values for back and crown colors (Figure 1), the hues of the back and crown are more similar to each other in nominate *trairllii* than in *campestris*; the back in *campestris* is greenish and the crown is grayish. Males of nominate *trairllii* and *campestris* differ slightly in relative lengths of primaries 10 and 5: $P10 > P5$ in 73% of *trairllii* ($n = 11$) and 94% of *campestris* ($n = 17$); $P10 = P5$ in 27% of *trairllii* ($n = 4$) and 6% of *campestris* ($n = 1$). Although the results for *campestris* are remarkably similar to those Unitt (1987) reported for his sample of *trairllii*, my small sample sizes indicate considerable overlap between the two subspecies for $P10 > 5$.

Specimens of nominate *trairllii* are much darker above than *extimus* and *adastus* and greener above than *brewsteri*. Nominate *trairllii* breeds from eastern Arkansas to southern Wisconsin, southern Illinois and Indiana, eastern New York (Syracuse), and Maine (Figure 2). Birds from eastern Tennessee (Siedman 1987, Tanner 1988), West Virginia (Hall 1983), and North Carolina (Potter et al. 1980), where the species is expanding its range, probably belong to the nominate subspecies.

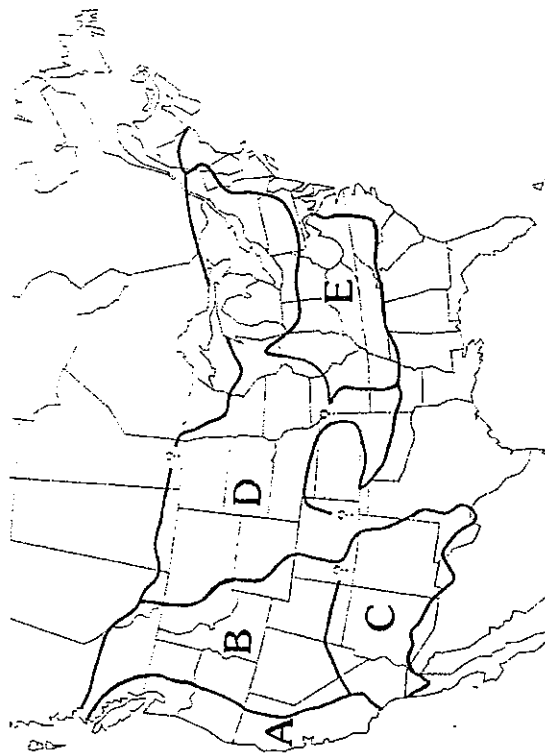


Figure 2. Approximate breeding ranges of subspecies of *Empidonax trairllii*: A, *brewsteri*; B, *adastus*; C, *extimus*; D, *trairllii*; E, *Empidonax alinum*; breeds north to Alaska.

Empidonax t. campestris. Stein's specimens of known song type from New York that sang fitz-bew (*E. t. campestris*, $n = 6$) are consistently much grayer on the crown and paler and grayish-green on the back than specimens that he indicated sang tee-bee-o (*E. alnorum*, $n = 4$).

Aldrich (1951) characterized *campestris* as darker and more greenish (less grayish or brownish) above than *extimus*, paler and greener (less brownish) above than *adastus*, and "considerably paler" than nominate *trairllii*. Most authors (e.g., Bailey and Niedrach 1965, Sittlon 1967, Oberholser 1974) who also recognized *campestris* characterized the subspecies as definitely paler above than *trairllii*.

I compared the holotype of *campestris* and 32 other specimens from the range of the subspecies (Aldrich 1951) with 20 specimens of *trairllii* from the northeastern and south-central U.S. I found that all specimens of *campestris* are paler and greener on the back, with paler crowns and cheeks, than specimens of *trairllii* (Figure 1). Specimens of *campestris* from western New York are darker above and on the breast than birds from North Dakota but are closer to *campestris* than to *trairllii*. The back of *campestris* is darker and slightly greener (less grayish brown) than that of *extimus*, and is paler and greener (less brownish) than that of *adastus*. I conclude that *campestris* should be recognized as a distinct subspecies.

According to Aldrich (1951), the breeding range of *campestris* includes central-eastern Arkansas, near the type locality of *trairllii*. Aldrich identified two breeding specimens from Stuttgart, Arkansas, only 37 miles northeast of the type locality of *trairllii*, as more similar to *campestris* than to *trairllii*. The two specimens are darker on the back, crown, and cheeks than *campestris* from North Dakota but paler and less brownish than specimens of *trairllii*. Fewer than 12 pairs breed near Stuttgart (James 1974). Willow Flycatchers no longer breed at the type locality of the nominate subspecies (D. James pers. comm., 1990), and additional specimens from Arkansas are not available. However, on the basis of specimens of *trairllii* from more eastern localities, I judge that the two Stuttgart specimens are intermediate between *campestris* and *trairllii*. The eastward expansion of the range of *campestris* (e.g., Aldrich 1953, Parkes 1954) may explain the intermediality of specimens near the type locality of *E. t. trairllii*.

Bailey and Niedrach (1965:522-523) believed that *campestris* was a migrant on the plains and foothills in Colorado east of the Rockies. Aldrich (in Bailey and Niedrach 1965) stated that there was no evidence of breeding on the plains of eastern Colorado, and identified specimens from the eastern slope of the Rocky Mountains as *adastus* that show a "tendency toward intergradation" with *campestris* in their "slightly paler and brownish" color. The species is now known to breed in Arapaho National Wildlife Refuge in north-central Colorado (Sedgwick and Knopf 1989). Available specimens from east of the Rockies in Colorado were collected in May and June and may not be on their breeding grounds. Such specimens from near the eastern slope of the Rockies, particularly from the Denver region, are slightly darker green above than most specimens of *campestris* from North Dakota and are more similar to but less grayish above than *adastus*. I tentatively consider specimens from Denver to represent *adastus*. Specimens from northeastern and southeastern Colorado, collected in late May,

resemble *campestris* from North Dakota. Specimens from just west of the Rocky Mountains in Summit County and from Garfield and Mesa counties, Colorado, are possibly intergrades between *adastus* and *extimus* (see beyond). I have been unable to locate two specimens from southeastern Idaho that Burleigh (1972) identified as breeding examples of *campestris*, but the specimens available from the same region are *adastus*.

Empidonax t. campestris breeds from southern Alberta and Saskatchewan to southern Ontario and Quebec south to probably central Texas, east-central Arkansas, northern Wisconsin, west-central Illinois, northern Indiana and Ohio, and eastern New York (Ithaca) (Figure 2). The western limit of *campestris* probably lies near the eastern slope of the Rocky Mountains from Montana to Colorado. Birds breeding in southern Manitoba (de Smet and Conrad 1988) and in the southern peninsula of Michigan (Pinkowski 1976) probably belong to this subspecies.

Empidonax t. extimus. Phillips (1948) characterized *extimus* as differing from *adastus* by being paler above, especially on the head, with the crown distinctly paler, the cheeks paler, the chestband less pronounced, and belly and crissum paler yellow. Many authors (e. g., Aldrich 1951, Behle 1985, Unitt 1987) have recognized this southwestern subspecies.

Two specimens from the southwestern U. S. collected since 1960 are pale grayish-green and older specimens are pale brownish above, usually with a breast band less distinct and paler gray than in the other subspecies. Specimens of *extimus* are paler above than those of other subspecies (Figure 1). Nominale *trairllii* is much darker above than *extimus*. Specimens of *extimus* resemble those of *campestris* but are more grayish and paler above in newer specimens and paler brown in older specimens.

A singing male from Pahrump Valley, Nye County, Nevada, collected 21 June, is referable to *extimus*. Two nonbreeding (N. K. Johnson pers. comm.) males from Ash Meadows, Nye County, collected on 15 June, are paler above but within the range of variation in *adastus*.

The breeding range of *extimus* is from northern Baja California (Unitt 1987) to southern California, southern Nevada (southern Nye and Clark counties), extreme southern Utah, Arizona, and New Mexico (Figure 2). I have not seen breeding specimens of *extimus* from Texas; *extimus* probably breeds (or bred) in western Texas between the Pecos River and the Rio Grande (Unitt 1987, but see Oberholser 1974).

Empidonax t. adastus. Oberholser (1932) characterized *adastus* as more grayish or greenish-brown above than *breusteri*. Miller (1941a) concluded that the range of variation in dorsal color in topotypical *adastus* was within that of *breusteri* and he, followed by Behle (1948), synonymized *adastus* with *breusteri*. On the other hand, Twomey (1942) and Behle (1958), the latter following Aldrich (1951) and others, recognized *adastus* as a distinct subspecies.

Miller (1941a:259) concluded that specimens from Oregon near the type locality of *adastus* and other birds from the Blue Mountains to the north were "exceedingly variable individually." I compared 26 specimens that likely were available to Miller (1941a) with other specimens of *E. trairllii*. Three specimens from Plush, Oregon (18 miles north of Adell), collected on 6 and 7 June, and a specimen from Wildcat Mountain, Crook County,

Oregon, collected on 16 June, are darker above and below than other birds from the series, and resemble specimens of *breusteri* from western Washington and Oregon. Testes of the three specimens ranged in length from 4 to 7 mm (mean 5.3 mm); testes of 8 paler specimens from the same regions ranged from 7 to 9 mm (mean, 7.9 mm). Because of the earlier dates, smaller testes, and darker color of the three specimens, I suspect that the birds were migrant *breusteri*. Although I agree with Miller (1941a) that individuals in the series vary from brownish to greenish above, the brownish birds are nonetheless paler and greener than specimens of *breusteri* (Figure 1). Furthermore, the crowns and edges of the tertials and secondaries are paler and the upper breasts are more grayish (less brownish) than in *breusteri* from western Washington and Oregon. Specimens from throughout the range of *adastus* vary somewhat in back color (Phillips 1948, pers. obs.); the colors of the rest of the plumage is constant. The subspecies is darker than *extimus*, especially on the crown and back. Linsdale (1951) reported that *breusteri* is a summer resident in Nevada, but the breeding specimens I examined, except from the extreme southern part of the state, are *adastus*.

The breeding range of *adastus* is from southeastern British Columbia to eastern California, and the Great Basin to the Rockies north of extreme southern Utah (Figure 2).

Empidonax t. breusteri. The northwestern subspecies *breusteri* is darker above than other western subspecies (Phillips 1948, Aldrich 1951, Unitt 1987, Figure 1). It differs from nominale *trairllii* by its browner back. Three males from southwestern British Columbia, two of which are near-typotypes of *zopholegus* (= *breusteri*), average slightly greener on the back and crown and browner on the upper breast than other specimens of *breusteri* from Washington to northern California. *Empidonax t. breusteri* breeds from southwestern British Columbia to western Washington and Oregon and the Sierra Nevada of Fresno County, California (Unitt 1987) (Figure 2).

Intergrades between *extimus* and *adastus*. Sites of reported intergradation between *extimus* and *adastus* include Clearwater and Nez Peace counties in central Idaho (Burleigh 1972), southern Idaho and northern Utah (Aldrich in Levy 1962), from southern Idaho and all but extreme southern Utah (Behle 1985), and probably the Rocky Mountains (Aldrich in Bailey and Niedrach 1965). Behle (1985) believed that birds from southern Idaho and Utah (excluding the extreme south) were intergrades but that these populations were more similar to *adastus* than to *extimus*. Unitt (1987:150-151) stated that the "reason for the varying identifications is that the intergradation between *extimus* and *adastus* in the Great Basin/Rocky Mountain area is much more gradual than that between *extimus* and *breusteri* in California." Although he cited Behle (1985), who concluded that there was a smooth cline from darker to paler birds in Utah, Unitt did not further discuss the zones of intergradation and included all of those populations under the subspecies *adastus*.

I compared 35 specimens from Utah, most of which were available to Behle, and 33 specimens from Idaho, most of which were examined by Burleigh, with 14 specimens of *extimus* from Arizona and New Mexico and

51 specimens of *adastus* from eastern Washington and Oregon. All of the specimens from north of extreme southern Utah are equally darker above than specimens of *extimus*. There is a geographic hiatus in Utah between the localities of the northernmost specimens of *extimus* and southernmost specimen of *adastus*. This hiatus is approximately 200 miles wide in western Utah and about 100 miles wide in the eastern part of the state. Thus, a gradual cline between *extimus* and *adastus* cannot be demonstrated.

Bailey and Niedrach (1965:522) listed five specimens from western Colorado collected in August under the subspecies *extimus* and, quoting Aldrich (in litt.), stated that *extimus* "probably enters some parts of western Colorado and intergrades with *adastus* in the Rocky Mountains." One of the August birds, from Garfield County, is *adastus*; although slightly worn, August specimens of *extimus* are usually paler than most August specimens of *adastus*. On the other hand, a bird from Summit County and one from Mesa County are pale above; they may be faded or represent intergrades between *extimus* and *adastus*.

Intergrades between *adastus* and *brewsteri*. Phillips (1948) reported intergradation between *adastus* and *brewsteri* from several localities in Oregon and stated that the area of intergradation occurs in "a good part" of western Oregon and California. In addition to the localities specified by Phillips (1948), I found intergrades between *adastus* and *brewsteri* from Oregon at Lookingglass (near Roseburg) in Douglas County (pale back and crown, with dark upper breast and edges of the tertials), several localities in Jackson County, and from northern California, in Siskiyou County from Hornbrook (two specimens with the edges of the tertials and upper breast dark, one with pale crown and dark back, and one with pale crown and paler back), and one from six miles northwest of Callahan on the Scott River (pale back with dark upper breast and edges of the tertials). In eastern Oregon, specimens from Ft. Klamath, Oregon, are browner above than *adastus* from Harney and Malheur counties but paler above and below than *brewsteri* from western Oregon. Because the specimens from Ft. Klamath are very old, I hesitate to identify them to subspecies. Although intergrades between *brewsteri* and *adastus* are known from a long north-to-south zone, I believe that interbreeding between the two subspecies is relatively limited and is similar to variation between currently recognized subspecies of other species that breed on both slopes of the Cascade Mountains and Sierra Nevada (see Miller 1941b, Browning 1974).

Phillips (1948) referred to the "headwaters of Drew Creek, Lake County, Oregon," as a place where darker and browner birds approach *brewsteri*. As noted by Phillips, this locality is "not far" (= ca. 60 miles) from the type locality of *adastus*. The subspecific characters of the only specimen from the headwaters of Drew Creek, collected in July, that I examined agree with Phillips' identification. However, this specimen is not geographically intermediate between the ranges of *adastus* and *brewsteri*; it is darker and browner than birds from Klamath Falls to the west and darker than birds to the east from the type locality of *adastus*. I believe that the bird from Drews Creek is either an extremely dark individual of *adastus* or possibly an example of *brewsteri* that was not on its breeding grounds.

SUMMARY

Audubon's *Muscicapa* (= *Empidonax*) *trairllii* is identifiable with the southeastern subspecies of the Willow Flycatcher. Five subspecies of *E. trairllii* are recognizable. Two breed east of the Rocky Mountains, *campestris*, with paler upperparts, in the Great Plains and Great Lakes regions, and nominate *trairllii*, with darker upperparts, to the southeast of this. Three breed west of the Rockies, dark brownish *brewsteri* from the Pacific Northwest south through the Sierra Nevada, intermediate *adastus* from the Rocky Mountains and intermountain regions, and pale grayish *extimus* from the southwest. Reports of intergradation between *adastus* and *extimus* in the Great Basin are incorrect. The breeding ranges of the five subspecies are not well known because of lack of known breeding specimens, both in the East, where the species is apparently expanding its range, and in the West, where ranges are contracting.

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