INTRODUCTION

The Willow Flycatcher is a common migratory species that breeds in a variety of usually shrubby, often wet habitats from Maine to British Columbia and as far south as southern Arizona and southern California. It winters from southern Mexico to northern South America in habitats similar to those occupied on the breeding grounds. Formerly considered conspecific with the Alder Flvcatcher (Empidonax alnorum), the 2 together were referred to as Traill's Flycatcher until 1973, when they were recognized as separate species (Am. Ornithol. Union 1957, 1973). As are most members of the genus Empidonax, Willow Flycatcher is difficult to identify in the field, and without vocal cues is nearly impossible to distinguish from Alder Flycatcher, whose habitats often overlap those of the Willow.

The Willow Flycatcher has been a much-studied species, partly because of its convoluted taxonomic history and similarity to the Alder Flycatcher and, more recently, because of the listing of the southwestern subspecies (E. traillii extimus) as Endangered (U.S. Fish Wildl. Serv. 1995). Studies of its morphology and plumage, behavior, nesting ecology, and song were all at least in part stimulated by the close similarity of the 2 vocal types (fee-bee-o and fitz-bew) of the (then) Traill's Flycatcher. Detailed investigations prompted by declining populations in the southwestern United States include those on the costs of cowbird parasitism, population dynamics, habitat preferences, and vocal and genetic differentiation across subspecific ranges.

Willow Flycatchers are late spring migrants and have a short, 70- to 90-day breeding season. This flycatcher is nearly always single-brooded, laying a clutch of 3 or 4 eggs in late May–late June; the incubation period is 13–14 days, and young fledge about 13–15 days after hatching, usually in mid-July, or somewhat earlier in the Southwest. Both adults feed nestlings and fledglings, but nearly always it is the female that incubates the eggs and broods the young. The Willow Flycatcher is primarily



Willow Flycatcher, adult at the nest



Figure 1. Distribution of the Willow Flycatcher in North and Middle America

an aerial forager, capturing most of its insect diet on the wing, but it may hover-glean extensively from leaf surfaces or occasionally take insects from the ground.

Because the Willow Flycatcher is restricted to river corridors (at least in the arid parts of the West), it is vulnerable to a variety of human activities that may alter or degrade such habitats, activities including river dewatering, channelization, overgrazing, dam construction, and urbanization. Breeding Bird Survey (BBS) data show this species decreasing in number in both the United States and the North American continent during the period 1966–1996 (Sauer et al. 1997).

In this account, most citations of studies published before 1973 (of "Traill's," "Western Traill's," "Little," or "Alder" Flycatcher; Am. Ornithol. Union 1931, 1957) refer to the Willow Flycatcher only, based on identity by vocalizations or range. In instances where species identity is in doubt, the superspecies name (Traill's Flycatcher) is used. See also Lowther 1999.

Distinguishing Characteristics

Small flycatcher, but relatively large for genus Empidonax —13.3–17.0 cm long (Godfrey 1986); 11.3–16.4 g mass (Dunning 1984). White throat contrasts with diffuse, dull olive to brownish breast band; bill wide and moderately long for *Empidonax*, entirely dull yellow-orange or pinkish on lower mandible and blackish on upper mandible (maxilla); whitish-gray wingbars (slightly buffy tips in fresh spring plumage) with anterior wing-bars often darker and duller than posterior. Upper parts drab olive, becoming brownish gray with wear; crown often darker due to dusky centers of coronal-feathers. Underparts light gray, washed with yellowish on the belly (spring); breast-band less distinct and belly less yellowish with wear; under wingcoverts white; indistinct (sometimes lacking), whitish eye-ring. Eye-ring, wing-bars, breastband most conspicuous in fresh, spring birds. Feet brownish black (Hoffmann 1927) to

(Pyle 1997a). blackish Sexes alike in appearance; during breeding season, males distinguished in hand by cloacal pro-tuberance and females by brood patch. Immatures browner above, yellower below, and wing-bars buff or vellowish brown and broader than in adults. Typical song a snappy FITZ-bew (note accent on first syllable); typical call simple, dry whit (see Sounds: vocalizations, below). Above description based on Jewett et al. 1953, Phillips et al. 1966, Whitney and Kaufman 1986, and Pyle 1997a.

Wood-pewees (members of genus *Contopus*) generally similar in plumage color and pattern, but slightly larger, with longer wings that extend farther down tail, longer primary extension (primaries showing beyond folded secondaries), more notice-ably peaked nape and crest, and different behavior of habitually returning to prominent perch (more so than *Empidonax*) and quivering wings but not flicking tail, unlike species of *Empidonax*.

Compared to other Empidonax, Traill's Flycatcher (Willow and Alder flycatchers) distinguished by large bill, indistinct or lacking eye-ring, no (usually) emargination of primary 6 (P6), wing morphol-ogy, and song (see Phillips et al. 1966, McKinney 1988, Pyle 1997a). Acadian Flycatcher (E. virescens) brighter green above, with pale yellowish eye-ring, much longer primary extension, and larger bill (longer and deeper). Other eastern species of Empidonax have short bills (e.g., Least Flycatcher, E. minimus). Dusky (E. oberholseri) and Gray (E. wrightii) flycatchers may be confused with Traill's, but both show whitish eye-ring (usually indistinct or lacking in western Willow), have narrow bills (Dusky with much of tip on lower mandible dark); Gray is paler and grayer than Traill's and exhibits characteristic downward, then upward tail flick. See Whitney and Kaufman 1986 and Natl. Geog. Soc. 1999 .

Willow and Alder flycatchers basically indis-tinguishable except by voice. Call of Alder usually an emphatic *pip* or *pit*, whereas Willow a liquid *whit* (see Sounds: vocalizations, below). Alder Flycatcher has a harsh, burry song with strongly accented second syllable, traditionally described as a 3-syllable *fee-BEE-o*, but which may be heard as a 2-syllable *rrree-BEEP* (sounds like *free-BEER!*), with the third syllable faint, indistinct (e.g., *rrree-BEEa*) or inaudible. Vast majority of nonvocalizing Willow/Aldertype *Empidonax* flycatchers should be identified only as Traill's Flycatcher. Identifica-tion without vocal cues requires attention to a combination of characters, including plumage pattern and coloration, linear measurements of wing (including lengths of primaries), bill, and tail. Properly aging and sexing (specimens or breeding condition differences) important.

In general, Alder has slightly greener crown, more pointed wings, slightly shorter bill, and slightly longer tail. Alder Flycatcher more readily separated from western forms of Willow Flycatcher (those populations west of western Great Plains, including subspecies E. t. brewsteri, E. t. adastus, and E. t. extimus), but not easily distinguished from eastern Willow Flycatcher (E. t. traillii). Compared to Alder and eastern Willow, western Willows generally paler with darker crown and browner back, tertials with diffuse (rather than sharply contrasting) internal border to pale edging, duller wing-bars not contrasting sharply with wing, indistinct or lacking eye-ring, and shorter primary projection (Natl. Geog. Soc. 1999). Eastern Willow similar to Alder Flycatcher in having greener back, distinct (sharply defined) pale edging to tertials. blackish wing with brighter wing-bars, and tendency to have eye-ring (though perhaps still less often or less distinct than Alder). At least some eastern Willows show grayer head contrasting with back, compared with greener crown not contrasting with back of Alder Flycatcher (P. Unitt pers. comm.).

Once above plumage characteristics determined, identification in hand aided by using the following formula developed by Stein (1963): D = 7.95 + 0.15 [(Plongest - P6) - (P5 - P6)]P10)] - bill length where Plongest is length of longest primary and P5, P6, and P10 are lengths of primaries 5, 6, and 10, respectively. Predicted identity is Willow Flycatcher if D is negative and Alder Flycatcher if positive. Only 68% and 79% of (sympatric) Willow and Alder flycatchers, respectively, identified correctly by this formula (Seutin 1991), even though Stein initially claimed to (1963)up 90.6% effectiveness. Because immatures have shorter bills than adults do, Hussell (1990) suggested a modification of Stein's equation (which is based

on adults) for classifying immatures (by dividing bill length of immatures by 0.961 before applying Stein's equation). Both authors recommend caution when using Stein's formula. Pyle (1997a) recommends a 15% buffer zone around the optimal equation (above) within which these 2 species should not be identified. More detailed examination of wing, tail, and bill measures provides another index --- "formula R" (Pyle 1997a, 1997b) — that also helps identify Alder and Willow flycatchers: R = [(Plongest -P6) + (P9 - P5) + (wing - tail)] / [(P6 - P10) +bill length]. 95% confidence intervals (CI) around R show little overlap between Alder Flycatchers (2.4–4.7 mm), eastern Willow Flycatchers (1.8-2.9 mm), and western Willow Flycatchers (1.0 - 2.2)mm). Multivariate discriminate function analysis, including values obtained from reflectance spectrophotometry (especially of crown color) corrected for age of specimen, measurements (especially wing shape), and plumage pattern (e.g., tertials and wing-bars) successfully distinguishes 100% of western Willows and >90% of eastern Wil-lows from Alders (P. Unitt and K. Messer unpubl.).

To some extent, there are slight differences in breeding-habitat preference and nest construction. Alder prefers wetter habitats with vegetation of lower height, and builds an untidy nest, often with straggling pieces of vegetation hanging beneath, placed low (usually <.9 m) and not over water; eastern Willow prefers dense stands of willow shrubs >2.1 m in height with moist soil or water beneath its neatly constructed cup that is placed about 1.2 m off ground.

Distribution

THE AMERICAS

Breeding Range

Figure 1. Most widely distributed North American *Empidonax*. Breeds north to the southern coast (east coast of Vancouver I. and Fraser Lowlands) and southern interior (Okanagan valley east to Alberta and north to Stum Lake) of British Columbia (Campbell et al. 1997), extreme sw. Alberta (Bow Valley, Jasper; Kulba and McGillivrav 2000), southernmost Saskatchewan (Missouri River tributaries; Smith 1996), sw. Manitoba, (sporadically; DeSmet and Conrad 1988), w. and s. Minnesota (mostly south of a line from Chicago to Stearns to Clay Cos.; Zink and Fall 1981), central and s. Wisconsin (south of a line from St. Croix Falls, to Waupaca, to Marinette, to Washington Is.; Robbins 1991), the lower peninsula of Michigan (most abundant southwest and southeast, and locally common in n. Lower Peninsula; confirmed breeding as far north as Alpina Co.; Payne 1991a), se. Ontario (common south of the Canadian Shield, sporadic farther north; Prescott 1987a), s. Ouebec (Central St. Lawrence Lowland; Seutin 1996), e. New Brunswick, Prince Edward Is., and possibly Nova Scotia (Erskine 1992). Breeds south to s. California (e.g., San Diego and Riverside Cos.; Small 1994), nw. and se. Arizona (south to Bill Williams and e. Gila Rivers and locally along the Colorado River south to confluence with w. Gila River; Paradzick et al. 1999), all but e. and southernmost New Mexico (Hubbard 1987), s. Missouri (Jacobs and Wilson 1997), s. Illinois, w. Kentucky (Palmer-Ball 1996), s. Tennessee (Nicholson 1997), extreme n. Georgia and mountains of w. North Carolina (Am. Ornithol. Union 1998), mountains of w. Virginia (Virginia Breeding Bird Atlas [BBA] unpubl.), central and w. Maryland (Van Ness 1996), and n. and coastal Delaware (Hess et al. 2000). Has bred occasionally south to ne. Louisiana (Am. Ornithol. Union 1998), n. Mississippi (Turcotte and Watts 1999), and w. South Carolina (McNair and Post 1993).

Sporadically distributed or absent from much of the Great Plains, including eastern half of Montana (Bergeron et al. 1992), ne. Wyoming (Dorn and Dorn 1990), w. South Dakota (Peterson 1995), sw. Nebraska (local in nw. Nebraska; Sharp et al. in press), Kansas (except extreme northeast; Kansas BBA 1992– 1997 unpubl.), eastern half of Colorado (absent east of foothills; Sedgwick 1998), southernmost and e. New Mexico (Hubbard 1987), Texas, and Oklahoma (Baumgartner and Baumgartner 1992).

Also absent from most of California with currently known breeding locations restricted pri-marily to Sierra Nevada/Cascade

region (se. Shasta Co. south to n. Kern Co., including Alpine, Invo, and Mono Cos.), near Buelton, Santa Barbara Co.; Prado Basin riparian forest, Riverside Co.; and several locations in San Diego Co. (Small 1994). Other conspicuous gaps in its distribution occur in Washington (absent from Central Columbia Basin; Smith et al. 1997), Nevada (occurs only in extreme north and south; T. Flyod pers. comm.), Tennessee (largely absent from w. and central portions; Nicholson 1997), Kentucky (largely absent from s.-central and easternmost parts of state; Palmer-Ball 1996), New Jersey (absent from Pine Barrens area; Walsh et al. 1999), New York (absent from Adir-ondack Mtns.; Bonney and Burrill 1988), Maine (restricted to easternmost portion of state; Adamus 1987). and New Hampshire (concentrated in coastal plain, rare in northern half of state; Berry 1994a).

Reported to be locally sympatric with Alder Flycatcher in central and w. New York; Garrett Co., MD; near Quakertown, PA; and Morris Co., NJ (Stein 1963). Also, in Connecticut (Litchfield Co.; Gorski 1969a, JAS), New Hampshire (Belknap, Johnson, and Rockingham Cos.; Berry 1994b), Vermont (Rutland and Addison Cos.; Kibbe and Norse 1985a), Minnesota (Clay, Wilkin, Anoka, and Pope Aitkin Cos.; Zink and Fall 1981), Michigan (Isabella Co.; Ewert 1981, Payne 1991b), Wisconsin (Adams, Marathon, Florence, Waukesha, and Walworth Cos.; Stein 1963, Robbins 1974), and Tennessee (Johnson Co.; Knight 1997).

In Canada, Alder and Willow flycatchers occur together in parts of British Columbia (Watson Lake to Williams Lake) and Saskatchewan (Cypress Hills, Qu'Appelle Valley and Souris River, Nicolle Flats; Stein 1963, DeSmet and Conrad 1988, Smith 1996), Alberta (Banff; Stein 1963), s. Ontario (Barlow and McGillivray 1983, Peck and James 1987, Prescott 1987b, Seutin 1987), near Montreal, Quebec (Seutin 1987), and s. New Brunswick (Erskine 1992).

Winter Range

Superspecies (Traill's Flycatcher) winters in Central and South America (Blake 1953), more specifically in Mexico (Coyuca), Guatemala (Los Amates. San Jose. Mazatenango). Honduras (Lancetilla, Ceiba), Nicaragua (San Carlos), Costa Rica (Bolson), n. and e. Colombia (Mamatoca, Bonda, Buritaca), nw. Venezuela (Encontrados), Ecuador (Gualaquiza, Zamora), e. Peru, n. and e. Bolivia, and nw. Argentina; vagrant to Amazon-ian Brazil (Bent 1942, Ridgely and Tudor 1994). Individuals identified as Willow Flycatchers by vocalizations reported as wintering in Mexico and Central America from Navarit, Mexico, south along Pacific slope to Costa Rica and Panama, along Atlantic slope from Honduras (possibly Veracruz, Mexico) south to Costa Rica, and in interior of s. Mexico (Balsas drainage) and interior of Costa Rica: although most numerous along Pacific slope (Ridgely and Gwynne 1989, Stiles and Skutch 1989, Howell and Webb 1995). Willow Flycatcher also reported as wintering south to nw. Colombia (Am. Ornithol. Union 1998). Some confusion as to how far south Willow Flycatchers winter owing to close morphological similarity to Alder Flycatcher and infrequent song on wintering grounds. Ridgely and Tudor (1994) report Willows tend to winter farther north in South America than Alders. Fitzpatrick (1980) gives winter range of Willows as s. Mexico (Veracruz, Oaxaca) to n. Colombia. Winter resident of Panama (response to tape 1969b) and Colombia playback; Gorski (specimens of all 4 subspecies; Wetmore 1972) from as early as 8 Sep to as late as 26 May. Cory and Hellmayr (1927) report wintering of the western races ("Western Traill's Flycatcher" [Empidonax traillii brewsteri Oberholser]) in s. Central America, Colombia, Venezuela, Peru, and Bolivia, with specimens from Guatemala, Costa Rica. Venezuela. and Colombia. Electronic colorimetry and wing measurements separate Willows and Alders (see to Distinguishing characteristics, above) revealed that Willow Flycatchers winter from Jalisco, Mexico (Pacific coast), and Guatemala (Atlantic coast) to n. Colombia and nw. Venezuela (P. Unitt and K. Messer unpubl.).

Other Records

Casual north to w., s.-coastal, and s. Alaska, and to central Ontario (Am. Ornithol. Union 1998).

OUTSIDE THE AMERICAS

Not recorded.

HISTORICAL CHANGES

E. t. extimus subspecies recently listed as Endangered (U.S. Fish Wildl. Serv. 1995). Historical declines in most parts of its range: in sw. Utah, once common in streamside willows (Salix spp.; Behle 1943) but now uncommon to rare (Whitmore 1977); once "abundant" in cottonwood and willow thickets along lowelevation streams in Arizona (Mearns 1890) and once the "commonest and characteristic species of its group" in Arizona (Coues 1874: 253). Now extirpated from much of its originally described range in Arizona (Unitt 1987). Formerly common and widely distributed in California riparian (Grinnell and Miller 1944). Now extirpated from most of its former California range (Harris et al. 1987) and rare to local in California riparian woodlands (Small 1994). Formerly bred locally in Trans-Pecos and Edwards Plateau of Texas (Oberholser 1974) and nw. Mexico (n. Baja California; Blake 1953, Unitt 1987, Am. Ornithol. Union 1998). Although recorded once during late Jun, no evidence that species has ever bred in Sonora, Mexico (Russell and Monson 1998). Also formerly bred locally in n. Arkansas, but by mid-1980s, breeders had disappeared from state (James and Neal 1986).

E. t. brewsteri once common the whole length of the Pacific Coast (Eliot 1923, Hoffmann 1927); formerly common and widely distributed in California up to 2,400 m in the Sierra Nevada and "wherever its special habitat exists" (Grinnell and Miller 1944: 256). Now rare to local in California mountain meadows (Small 1994). Only about 200 Willow Flycatcher pairs breed in California (140-150 in Sierra Nevada = *E. t. brewsteri* and remainder in s. California = E. t. extimus; Small 1994; also, see Conservation and management: effects of human activity, below). Species expanding northward in Ontario (E. t. traillii), possibly at the expense of Alder Flycatchers, owing to wetland drainage and colonization of abandoned pastures by small trees and shrubs (Stein 1963;

Prescott 1987a, 1987b); but in Wisconsin, Alders may have extended range into Willow Flycatcher areas (Robbins 1974); this may also be happening in British Columbia (Campbell et al. 1997). In New York, due to removal of original forest cover, Willows have expanded their range from the west along the plain of the Great Lakes and from the south up the lower Hudson Valley (Parkes 1954). Willows began to spread into Vermont from the south and southwest during 1960s (Norse 1985).

Breeding range of Willow Flycatcher has also expanded southward in e. and se. U.S., including Ohio (now occurs statewide, but formerly restricted to northern half of state: Peterjohn 1989), Pennsylvania (previously rare in west and southeast, but now a common breeder; Mulvihill 1995), Kentucky (formerly uncommon, now regular at scattered localities; Palmer-Ball Jr. 1996), Tennessee (first nesting record in 1958, but now breeds across a broad front; Nicholson 1997), W. Virginia (invasion began in 1930s; Hall 1983), and Maryland (main increase began in 1960s; Van Ness 1996). Additional first state breeding records for the Southeast include S. Carolina, Spartanburg Co., Jun 1991 (McNair and Post 1993), and Mississippi, Tallahatchie Co., Jul 1996 (Turcotte and Watts 1999).

Fossil History

No data.

Systematics

Formerly regarded as song form of Traill's Flycatcher until 1973 (Am. Ornithol. Union 1973) when partitioned into: (a) Willow Flycatcher (*Empidonax traillii* Audubon 1828), defined as the "*fitz-bew*" song form of those populations of the former *E. t. traillii* of prairies and open habitats of the Midwest and e. U.S., and *E. t. brewsteri* of w. U.S.; and (b) Alder Flycatcher (*Empidonax alnorum* Brewster 1895), defined as the "*fee-bee-o*" song form of populations of former *E. t. traillii* of boreal regions of Alaska, Canada, and e. U.S. Names used in older literature for Willow Flycatcher

include Muscicapa traillii Audubon 1828, Platvrhvnchus Swainson 1827, pusillus Empidonax pusillus, Empidonax traillii brewsteri Oberholser 1918, Empidonax traillii adas-tus Oberholser 1932, Empidonax traillii zopholegus Oberholser 1947, Empidonax traillii extimus Phillips 1948, and Empidonax traillii campestris Aldrich 1951. Names and synonymy for Alder Flycatcher include Empidonax traillii alascensis Phillips 1948 and Empidonax traillii alnorum Brewster 1895 [synonymized as Empidonax traillii Audubon 1928 by Oberholser (1918), Phillips (1948), Aldrich (1951), and Stein (1963); but see Eisenmann (1970). Am. Ornithol. Union (1973), and Browning (1993)]. Some authors accept Empidonax traillii Audubon 1928 as the proper name for the Alder Flycatcher and use the name Empidonax brewsteri Oberholser 1918 for the Willow Flycatcher.

GEOGRAPHIC VARIATION

Geographic variation observed in plumage pattern and coloration, wing morphology, and vocalizations; no evidence of variation in size per se (wing-chord, tail, or bill; Unitt 1987, Browning 1993, Sedgwick in press). Two broad groupings based on plumage pattern and coloration (see differences described for western and eastern forms of Willow Flycatcher in Distinguishing characteristics, above). East-towest trend in wing morphology (eastern forms have more pointed wings) and an apparent correlation between plumage color and humidity. Willow Flycatchers lightest in arid sw. U.S. and on Great Plains and Upper Midwest; darkest forms occur in more humid e. and se. U.S. and in Pacific Northwest. For western populations, variation in song is correlated with both latitude and elevation. Compared to southerly, lower-elevation populations, northern, higher-elevation Willow Flycatchers tend to have slightly higher-pitched and shorter *fitz-bew* songs, with a more rapidly modulated final element.

SUBSPECIES

Authors recognize either 4 or 5 subspecies (E. t. traillii, E. t. adastus, E. t. brewsteri, E. t. extimus, and some also recognize E. t. campestris; Phillips 1948, Aldrich 1951, Hubbard 1987, Unitt 1987, Browning 1993). Plumage coloration and wing morphology have so far proven to be most useful characters to define Willow Flycatcher subspecies. From darkest to lightest plumage (back and crown), the subspecies may be ordered E. t. traillii, brewsteri, adastus, campestris, and extimus (Browning 1993, but see Hubbard 1987). Western subspecies (extimus, adastus, and brewsteri) can be distinguished (mostly) from the eastern subspecies (traillii, campestris) on basis of wing formula (eastern, $P10 \ge P5$; western, $P10 \le P5$) and plumage pattern and coloration (see above), but not from one another. The 3 western subspecies also distinguished by indistinct (buff to whitish) wing-feather edging compared to bright (whitish to lemon yellow) wing-feather edging in eastern subspecies (Pyle 1997a); in eastern subspecies, edgings on tertials also brighter (whiter contrasting with darker, blacker background) with sharply defined internal border. Apart from these broad groupings, there is considerable overlap between subspecies with clinal variation and intergradation near subspecific range boundaries, com-plicating taxonomic partitioning (see below). As a result, and because of a lack of breeding specimens, some subspecific range boundaries for Willow Flycatcher are poorly delimited; evolutionary relationships little studied. Distributions given (further, below) based mostly on Browning 1993, but also on Phillips 1948, Am. Ornithol. Union 1998, and Unitt 1987.

After Sedgwick in press. Differences in song have been investigated only recently and may prove useful in making taxonomic inference and delimiting subspecific ranges. In w. U.S., low-elevation, southerly desert populations of *E. t. extimus* (Arizona, New Mexico, and s. Utah) have a unique vocal identity differing from that of more northerly song groups of *E. t. adastus* (Oregon, Colorado, and n. Utah). These 2 subspecies sort out by

both latitude and elevation: birds with the vocal identity of southern populations can occur as far north as 37°N if at low elevation, and those acoustically similar to northern populations can occur as far south as 33°42'N if at high elevation. Song type does not appear to be broadly clinal, but the vocal background of birds in zones of contact (e.g., n. New Mexico) is intermediate, suggesting intergradation. Pure forms of E. t. extimus apparently do not occur in Colorado, as even the southernmost populations in Colorado are acoustically similar to more northerly populations known to be *adastus*. A low-elevation population in w. Colorado stands apart from other *adastus* populations, suggesting moderate introgression of extimus genes into the adastus gene pool.

E. t. traillii (Audubon, 1828): Southern range limits fairly well known (south to n. Arkansas [rare], n. Tennessee, S. Carolina [rare], n. Georgia, w. North Carolina, and east to central Virginia), but boundary abutting *E. t. campestris* to the north and east less certain (breeds Maine; New Hampshire; west to e. New York; north to s. Pennsylvania, s. Ohio, s. Indiana, and s. Wisconsin; and west to w. Illinois, central Missouri, and central Arkansas (Fig. 1, after Browning 1993). Darker, less greenish, and more brownish (back and crown) than *campestris*; greener above than *brewsteri*; much darker above than *extimus* and *adastus*; extensive overlap with *campestris* in wing morphology (both, P10 \geq P5). Intergrades between traillii and campestris reported from Arkansas (Browning 1993).

E. t. campestris Aldrich, 1951: Some synonymize this subspecies with *E. t. traillii*. Range boundaries with *E. t. traillii* unclear (see above); breeds north to s. Canada from s. Ontario and Quebec to s. Alberta and Saskatchewan; western limit near east slope of Rockies from Colorado to Montana. Paler and greener on back, and with paler crown and cheeks than *traillii*; back paler and greener than *adastus* but darker and greener than *extimus* (Browning 1993).

E. t. adastus **Oberholser, 1932**: Breeds from s. British Columbia to e. California (east of Cascades and Sierras), and in the Great Basin to the Rockies, north of extreme s. Utah. Paler and greener above, upper breast more grayish, and edges of tertials and secondaries paler than in *E. t. brewsteri*; darker above than *extimus* . Intergrades between *adastus* and *extimus* reported from central and s. Idaho, n. and central Utah, and the Rockies of Colorado (Bailey and Niedrach 1965, Burleigh 1972, Behle 1985; but see Browning 1993).

E. t. brewsteri Oberholser, 1918: Occurs west of the Cascades and in the Sierra Nevada from sw. California up to sw. British Columbia; boundary between *brewsteri* and *adastus* to the east uncertain. Darker above than other western subspecies, browner-backed than *traillii*, and browner or more olive than *E. t. adastus* (Unitt 1987, Browning 1993). Intergrades between *adastus* and *brewsteri* reported from w. to central Oregon and in n. California (Phillips 1948).

E. t. extimus Phillips, 1948: Breeds in the Southwest, including s. California, Arizona, New Mexico west of the Rio Grande, sw. Utah, s. Nevada, and possibly sw. Colorado (Unitt 1987, Browning 1993). Paler on back and especially on head than either *E. t. adastus* or *E. t. brewsteri*; breast-band less distinct and paler gray than in other subspecies (Browning 1993). Northern extent of pure forms of *E. t. extimus* in New Mexico remains unclear, as does whether *E. t. extimus* occurs as far north as sw. Colorado (JAS); song forms intermediate to *adastus* and *extimus* occur in n. New Mexico and possibly in w. Colorado (Sedgwick in press).

RELATED SPECIES

Most closely related to Alder Flycatcher. Although distinct vocally and in features of nesting biology, Willow and Alder flycatchers appear to share an identical chromosomal morphology (karyotypes; Shields et al. 1987); the genome size of their mitochondrial DNA (mtDNA) is similar (16,600 base pairs \pm 300 SE; Winker 1994). Electrophoretic analysis of

proteins confirms the close relation-ship of E. traillii and E. alnorum; genetic distances between the 2 species among the lowest reported for avian species (mean Nei's distance [D] between heterospecific samples = 0.009 [Zink and Johnson 1984] and = 0.004 [Seutin and Simon 1988]). This is an order of magnitude lower than for most congeners (avian average = 0.044 [Barrowclough 1980]; average between 11 species of *Empidonax* = 0.070 [Zink and Johnson 1984]). Low genetic differentiation at the protein level however, "should not be taken as evidence for conspecificity" (Seutin and Simon 1988: 241) but suggests that Alder and Willow Flycatchers should be regarded as species pairs (Zink and Johnson 1984). Nucleotide sequence divergence ($p = 0.055 \pm$ 0.13; mtDNA genetic distance) between Alder and Willow flycatchers, on the other hand, is higher than that of several other avian-sibling species pairs that have been compared so far (Avise and Zink 1988, Winker 1994).

Genus *Empidonax* placed in subfamily Fluvicolinae and probably most closely related to pewees (*Contopus*) among that group of tyrannids (Zink and Johnson 1984).

Hybridization

No evidence of interbreeding with Alder Flycatcher (Stein 1963, Gorski 1970, Seutin and Simon 1988, Winker 1994), although Stewart (1975: 180) reported some songs of territorial males in North Dakota "seem to be somewhat intermediate" between typical Willow and Alder songs. Because of the 2 species' close relationship, phenotypic similarity, and similar habitat preferences, Winker (1994) and Seutin and Simon (1988) predicted that hybridization would be likely. A comparison (no mismatches) of mtDNA and song type suggested an absence of hybridization, however (Winker 1994). And in a study of sympatric and allopatric Willow and Alder flycatcher populations in se. Canada, there were no significant differences in the levels of genetic variability (numbers of polymorphic loci and levels of heterozygosity) of the populations, suggesting inter-breeding does not occur or at least does not occur at high frequencies (Seutin and Simon 1988). Interspecific competition at sites of syntopy and

recognition and aggressive response to heterospecific song (Prescott 1987b) apparently have acted to maintain genetic isolation in areas of contact (Winker 1994). Similarly, both Stein (1963) and Gorski (1970) found that the 2 species did not inter-breed when sympatric. Barlow and McGillivray (1983), however, found no evidence of interspecific aggression, nor of response to playbacks of the other's song and attributed this either to high resource abundance or insufficient time since secondary contact.

One instance of an intergeneric hybrid Willow Flycatcher \times Western Wood-Pewee (*Empidonax traillii* \times Contopus sordidulus), suggesting close similarity of genomes of species in those 2 genera (Short and Burleigh 1965; see also Zink and Johnson 1984).

Migration

NATURE OF MIGRATION IN THE SPECIES

Long-distance migrant; completely migratory. Breeds in U.S. and s. Canada and winters in s. Mexico, Central America, and n. South America. Migration likely nocturnal based on tower-kill data (e.g., Crawford 1976). A very late spring migrant with spring and fall dates of passage similar to those of Alder Flycatcher (Hussell 1991a, 1991b).

TIMING AND ROUTES OF MIGRATION

Spring

In Mexico and n. Central America, Willow Flycatcher is spring passage migrant Apr–early Jun; mostly on Pacific slope, less common interior and Atlantic slope (Howell and Webb 1995). Stevenson (1957), however, reported that *Empidonax* flycatchers are "quite common" in spring in e. Mexico. Because of paucity of records from islands in the Caribbean during spring (McCabe 1991 and references therein), because there are no spring specimen records (Phillips and Lanyon 1970, Crawford 1976) and no Bird Banding Lab spring records for Florida (BBL files), and because Willow Flycatchers are

not strong flyers, a circum-Gulf of Mexico, rather than a trans-Gulf or an island-hopping migration north seems more likely for eastern populations of Willow Flycatcher (McCabe 1991); needs more study.

In Connecticut: Earliest spring arrival is 13 May (Zeranski and Baptist 1990). Iowa: Early spring date 5 May (Kent and Dinsmore 1996). Michigan: Average spring arrival 17 May (Walkinshaw 1966). Minnesota: Traill's Flycatcher, 5–29 May, median 23 May (Winker et al. 1992). Wisconsin: 15 May usual first date (Robbins 1991), but McCabe (1991) gave 1 May and 29 May as earliest and latest arrival dates with a mean of 15 May. Illinois: Earliest specimen 3 May, with migration extending well into Jun (Graber et al. 1974). Ohio: Most of spring passage 20 May-5 Jun (Peterjohn 1989). Ontario: Spring migration essentially complete by 10 Jun, with 90% of spring migrants 21 Mav-9 Jun (Hussell 1991a).

In Arizona: *Extimus* subspecies first to arrive (earliest, 3 May; Phillips et al. 1964). California: Late spring transient from second week of May to mid-Jun (Small 1994). Colorado: Early arrival 18 May (Bailey and Niedrach 1965). Wyoming: Uncommon summer resident from 7 May (Dorn and Dorn 1990). Kansas: For Traill's Flycatcher, spring migration peaked 20–25 May (87% of all birds captured); most captures during periods of inclement weather (Ely 1970). Oregon: Average spring arrival date in se. Oregon (Malheur National Wildlife Refuge [NWR]) 12 May (extreme 29 Apr; Littlefield 1990).

Fall

Recorded widely as a fall migrant in s. U.S. (Am. Ornithol. Union 1998), but (eastern subspecies) "shuns the se. United States south of North Carolina" (Cooke 1908: 115). Despite its scarcity in the Southeast, the species occurs more frequently along the entire Atlantic Coast in fall than during spring. In Florida, for example, the superspecies is a rare fall migrant (20 Aug–19 Oct) but casual spring migrant (Fisk 1971, Crawford 1976, Stevenson and Anderson 1994). Eastern populations then appar-ently exhibit a westward autumn migrational swing and become part of either a circum-Gulf or trans-Gulf migration pattern en route to Central

and South America (McCabe 1991). Fall tower kills in Florida (Crawford 1976) and the occurrence of fall migrants in Cuba and Jamaica (very rare; Raffaele et al. 1998) suggest, however, that at least a small proportion take an island-hopping route across the Caribbean to Central and South America. Willow Flycatchers breeding in central and w. U.S. likely migrate (overland) more or less straight south en route to their wintering grounds. In Mexico and n. Central America, fall passage migrant Aug–Oct mostly on Pacific slope; less common in interior and on Atlantic slope (Howell and Webb 1995).

In Connecticut: Latest fall departure 29 Sep (Zeranski and Baptist 1990). Vermont: 74% of captures (Traill's Flycatcher) 16 Aug-2 Sep (Kibbe and Norse 1985a). Iowa: Late date 25 Sep (Kent and Dinsmore 1996). Minnesota: Traill's Flycatcher, 17 Aug-21 Sep, median 28 Aug (Winker et al. 1992). Michigan: Few birds present after 10 Aug (Walkinshaw 1966). Arizona: Extimus subspecies lingers until 10 Sep (Phillips et al. 1964). California: Fall migration peaks from mid-Aug to mid-Sep; com-mon fall transient along California coast (Small 1994). Colorado: Late departure 19 Sep (Bailey and Niedrach 1965). Wyoming: Uncommon summer resident to 14 Sep (Dorn and Dorn 1990). Kansas: Fall migration (Traill's Flycatcher) 23 Jul-12 Sep. Oregon: Fall migration peaks late Aug east of Cascades, early Sep west of Cascades (Gilligan et al. 1994).

MIGRATORY BEHAVIOR

Generally nocturnal. Known to be a night migrant in Illinois (Graber et al. 1974) and from tower-kill data (Crawford 1976). Males tend to migrate earlier in spring than females (Hussell 1991a, M. Whitfield pers. comm.); arrive in Michigan over a 10–14 d period (Walkinshaw 1966). King (1955), however, suggested sexes arrive almost simultaneously in se. Washington.

In fall migration, adults precede immatures (Unitt 1987, Yong and Finch 1997), likely because young birds' Prebasic molt occurs on breeding grounds (adding to length of their stay), whereas adults delay Prebasic molt until they reach win-tering grounds (but see Appearance: molts and plumages, below). Similarly, middle 90% of adults at Long Point, Ontario, occurred 17 Jul–23 Aug, whereas middle 90% of immatures occurred 11 Aug–9 Sep (Hussell 1991b). Fall migration of immatures, at least, stimulated by decline of supply of aerial insects on breeding grounds (Hussell 1991b).

CONTROL AND PHYSIOLOGY

Fall migrant Traill's Flycatchers on Appledore I., Maine (1983–1992) gained an average of 1.5 $g \pm 1.7$ SD, or a 12.1% increase in mass, during an average stopover of 2.9 d \pm 1.7 SD (range 1– 7, n = 428 captures, 37 recaptures; Morris et al. 1996). In California, 76% of fall migrant Willow Flycatchers (n = 340) showed no visible fat deposits; mean stop-over length 6 d \pm 3.7 SD (range 2–19, n = 37); mean mass change 0.7 g/d \pm 0.3 SD (range -0.6–0.5); estimated increase in flight range from stopover mass gain 158 km (Otahal 1998). Spring and fall migrants through New Mexico (n = 84) had fat stores ranging from 0% (no fat, 49% of individuals), to 8% (1.0 g fat, 39% of individuals), to 20% (2.4 g fat, 12% of individuals) of fat-free mass; recap-tured birds (n = 7) had average body-mass gain of 1.6%/d (Yong and Finch 1997). This translated into a mean potential flight range of 225 km (all fat classes combined) and a mean for highest fat classes of 404 km; thus, most Willow Flycatchers would have been unable to reach their breeding grounds in a single flight, making it necessary to stop again en route and replenish fat stores.

Habitat

BREEDING RANGE

In general, prefers moist, shrubby areas, often with standing or running water; e.g., in California, "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" (Grinnell and Miller 1944: 257). An affinity for moist or wet shrubby situations noted throughout the West (Dawson 1923, Gabrielson and Jewett 1940, Hand 1941, Sumner and Dixon

1953). An exception occurs in Palouse Prairie of se. Washington where, in addition to mesic riparian sites, also nests in xeric uplands, including dry, brushy prairie remnants containing hawthorn (Crataegus spp.), chokecherry (Prunus spp.), or rose (Rosa spp.), and dry ninebark (Physocarpus sp.) thickets (King 1955). In central and e. U.S., uses both wet sites and dry, upland sites (Campbell 1936, Aldrich 1953, Berger 1957, Stein 1963, McCabe 1991, JAS). In the Southwest, occurs in riparian forests with or without shrubs (M. Whitfield pers. comm.).

In the West, generally occurs in beaver meadows, along borders of clearings, in brushv lowlands, in mountain parks, or along watercourses to 2,500 m (Hoffmann 1927, Bent 1942, Jewett et al. 1953). In Colorado, occurs in foothills, lower mountains, and in open valleys and mountain parks; rare in lowlands (Andrews and Righter 1992). Occurs in moderate density in early-growth clearcuts in Oregon (Morrison and Meslow 1983). In California, high foliagevolume willow cover preferred but with willow clumps separated by openings (Harris et al. 1987); in Sierra Nevada, 46% ± 23% SD of territory covered by willow clumps (n = 8; Flett and Sanders 1987). In British Columbia, in addition to riparian habitat, occurs in 30- to 35yr-old forests (red alder [Alnus rubra] thickets), woodlands near agricultural land, dry hillsides of aspen (Populus tremuloides) parklands, and clearcuts in early regeneration (Campbell et al. 1997). In desert Southwest, the only Empidonax to breed along wooded desert streams (Oberholser 1974). A relative habitat generalist on the Colorado River, preferring vegetation with high foliage volume and few trees (Brown and Trosset 1989); along Virgin River in sw. Utah, also confined to areas of few trees and high shrub density, but described as a habitat specialist (Whitmore 1977).

In prairie states, an edge-adapted species asso-ciated with low gallery forests along streams, prairie coulees, riparian habitats, and woodland edge (farther north) such as muskegs and boggy openings (Johnsgard 1986). In Illinois, prefers wet areas with willow clumps, upland shrub areas, and roadside shrubs and hedges (Graber et al. 1974). In Ohio, may occur in wet, brushy habitats with Alder Flycatcher, but more likely to occupy dry upland areas (Peterjohn and Rice 1991).

In a Colorado study, microsite habitat prefer-ences of males (song perches) and females (nests) differed: Females preferred areas of high willow density and a uniform willowpatch size and height; males preferred areas with a large, decadent, song-perch shrub and surrounding shrubs of variable size (Sedgwick and Knopf 1992). Females shown to be more discriminating in habitat selection than males: Their microhabitat differed more from unused habitat than did that of males, and at the smallest scale measured, male habitats more similar to unused than to female microhabitats (Sedgwick and Knopf 1992). See also Breeding: nest site, below.

SPRING AND FALL MIGRATION

Generally similar to breeding habitat (McCabe 1991). Throughout riparian woodlands in the West, including shrub willow, cottonwood (*Populus*), and Russian olive (*Elaeagnus angustifolia*); also through adjacent agricultural fields (Yong and Finch 1997). In New Mexico study along Rio Grande, willow habitat had highest capture rate, and individuals captured in willow habitat had highest average body mass compared to cottonwood, Russian olive, and agricultural fields (Yong and Finch 1997); this presumably due to higher arthropod densities in willow habitat.

WINTER RANGE

Shrubby clearings, pastures, and lighter woodland; often near water. In Amazonia, on river islands with early-successional growth, mostly below 1,000 m (Ridgely and Tudor 1994). Arid scrub preferred; woodland edge, brushland, humid brush, and pastures less preferred (Fitzpatrick 1980). In Panama, wet, open grassy areas in transition to shrubby areas interspersed with trees, as well as thickets and forest borders (Gorski 1969b, Wetmore 1972); fairly common to common and often near water (Ridgely and Gwynne 1989). In Mexico and n. Central America, uses humid to semiarid scrubby fields with hedges, fences, woodland, and fields, from sea level to 2,500 m (Howell and Webb 1995); chiefly in coastal lowlands in Mexico (Edwards 1972); common in lowlands of El Salvador (Dickey and van Rossem 1938).

Food Habits

FEEDING

Main Foods Taken

Primarily insects; occasionally fruit.

Microhabitat For Foraging

In Colorado, willows favored foraging perch sites; favored foraging substrates were air, willows, and sedges (Eckhardt 1979). Primary gleaning substrates in Washington were leaves, herbs, grass, flowers, and conifer branches (Frakes and Johnson 1982). In se. Oregon, most foraging in cattail (*Typha* sp.) marshes adjacent to willow riparian nesting areas but also in openings between willow patches and over water (JAS). Occasionally forages from ground.

Food Capture And Consumption

Primarily an aerial forager, including both hawking and hover-gleaning. In Washington, frequency of gleaning ranged from 35.2 to 45.7% (n = 230) and in Ontario from 37 to 63% (n = 1.058; Frakes and Johnson 1982, Barlow and McGillivray 1983). Preferred horizontal (versus ascending or descending) foraging flights, of short length from perch to point of capture (usually <3 m), from low perches (1–3) m; Frakes and Johnson 1982). Willow and Cordilleran [*E*. occidentalis] flycatchers converged in their foraging niches when occupying the same habitat, indicating that both can change certain aspects of foraging behavior from one habitat to the next. Foraging ecology of Willow and Alder shows extensive overlap whether breeding allopatrically or sympatrically (Barlow and McGillivray 1983).

In Ontario, spent only 5% of time foraging, but 63% perched (Prescott and Middleton 1988); thus this species is a "time minimizer," able to simultaneously engage in foraging, territorial advertisement, vigilance, and resting. Eckhardt (1979), however, noted that foraging velocity (number of perches/unit time) decreased dramatically during singing periods, suggesting that searching for food and singing cannot occur simultaneously. Foraging intensity (number of attacks/unit time) also de-creased during singing, leading Eckhardt (1979) to reject the notion that territorial defense can be performed within the context of normal search behavior in this species.

DIET

Major Food Items

Mostly insects.

Quantitative Analysis

Mostly (96%) animal; Hymenoptera (bees, wasps, and ants; 41%), Cole-optera (beetles; 18%), Diptera (flies; 14%), Lepid-optera (butterflies, moths; 8%), and Hemiptera (true bugs; 7%) most common; vegetable matter mostly in Sep and largely various berries (blackberries and raspberries [Rubus spp.], dogwood berries [Cornus spp.]; n = 135specimens; includes Alder Flycatcher; Beal 1912). In Wisconsin, adult foods include dragonflies (Odonata), ichneumon flies (Ichneumonidae), deer flies (Tabanidae), hemipterans, and lady bugs (Coccinellidae; 1991). In Ontario. McCabe damselflies (Odonata) frequently taken by adults (Prescott and Middleton 1988). Individual food items identified in se. Oregon include dragonflies, damselflies, horseflies (Tabanidae), Ribes berries, and cabbage butterflies (Pieridae; JAS).

Composition of nestling diet (by using neck ligatures) in an Ontario study was dominated by Diptera and Hemiptera but also included Mollusca (mollusks). Arachnida (primitive crustaceans), (spiders), Isopoda Orthoptera (grasshoppers, crickets), Coleoptera, Lepidoptera, and Hymenoptera (n = 333)vertebrates; Prescott and Middleton 1988). In 214 food samples retrieved from nestlings in 8 nests in Wisconsin, McCabe (1991) identified insects from 33 families, the 5 most common being Tabanidae (deer flies), Syrphidae (syrphid flies). Hesperiidae (common skipper), Cercopidae (spittlebug), and Scarabaeidae

(scarab beetle). On wintering grounds, only insects were found in stomachs examined by Wetmore (1972); some fruit noted in feces samples from Costa Rica (T. Koronkiewicz pers. comm.).

FOOD SELECTION AND STORAGE

Not known to store food.

NUTRITION AND ENERGETICS

No data.

METABOLISM AND TEMPERATURE REGULATION

No information.

DRINKING, PELLET-CASTING, AND DEFECATION

Presumably obtains adequate water needs from insect diet; drinking not reported. Pellet-casting not uncommon; perched Willow Flycatchers observed with gape open wide and expelling oval pellets (about \leq 5 mm diameter) presumably composed of carapaces, legs, and other hard body parts of insects (JAS). Defecates several times/hr throughout day (JAS).

Sounds

VOCALIZATIONS

Development

Song of Willow Flycatcher innate and not learned as in oscines (Kroodsma 1984). Willow Flycatchers reared from 7–10 d of age in acoustic isolation, and even those tutored with Alder Flycatcher songs, produced conspecific songs similar to wild-type songs (Kroodsma 1984). Ability to sing Advertising Song develops as early as 6–8 wk of age; 1 individual identified as a juvenile responded to tape playback with several soft *fitz-bews* in Arizona (Sogge 1997).

Vocal Array

Advertising-Song performance consists of 3 vocalizations: *fitz-bew*, a similar-sounding *fizz-bew*, and *creet*. *Fitz-bews* are given most frequently (42.9%), followed by *creets* (32.4%) and *fizz-bews* (24.7%; n = 786 vocalizations; 13 song bouts from 13 individuals; JAS).

Song performance is mostly by males; females also sing, but this is thought to be uncommon. In se. Oregon (E. t. adastus), of confirmations of territorial hundreds ownership of color-banded, singing Willow Flycatchers all proved to be males (JAS); Gorski (1970) reported that only males responded to playback with song, whereas females displayed less aggressive behavior and uttered only alarm notes. In Ontario and Quebec, however, 4 of 21 Willow Flycatchers singing in response to tape playback were later determined to be females; among the 4 females, all 3 forms of the Advertising Song were given (Seutin 1987). One of the 4 females was singing spontaneously before tape playback began and was singing at the top of a willow bush. In s. California, occasional female song noted (M. Whitfield pers. comm.). Most birds heard singing in the field and believed to be females do so from lower perches within a bush and give only weak



Figure 2. Songs and calls of the Willow Flycatcher

versions of the Advertising Song (JAS). Sogge et al. (1997) reported 1 individual believed to be a female singing over a period of 40 min while her mate and a neighboring male were countersinging; she sang from near the nest and 5 times while sitting on the nest.

A sharp, snappy song with accent on first syllable; can sound similar to song of Alder (fee-BEE-o) but accent of Alder song is on second syllable (Fig. 2A; Whitney and Kaufman 1986, Ridgely and Tudor 1994). Alder pit and wee-oo calls given together can sound superficially like *fitz-bew* of Willow Flycatcher (Stein 1963); late in breeding season, 2-note Alder songs, where last syllable is inaudible or not produced, can be confused with Willow songs (Campbell et al. 1997); even at other times of year, third Alder song syllable can be hard to detect (Whitney and Kaufman 1986). "Fitz " syllable composed of 2 elements, first slurred upward and second downward; " bew " made up of 3 sections: 2 or 3 widely spaced introductory notes, a midsection that is modulated rapidly in frequency, and a third section that is modulated more slowly (JAS). Fitz-bew vocalization of E. t. extimus recognizably different from that of other subspecies; sometimes described as a fitzbew with a slow, Southern drawl. Most obvious spectrographic difference is in last section of " bew ": " Bew " of E. t. extimus has fewer notes and these are modulated more slowly than in the other subspecies (Fig. 2B; Sedgwick in press; also, see Systematics: geographic variation, above).

Sounds very similar to *fitz-bew*; begins (*fizz*) with a series of ascending, closely spaced notes; followed by a *bew* that is similar to the "*bew*" of the *fitz-bew*, but contains only 1 or 2 introductory notes; midsection begins at a higher frequency and last section descends more in frequency than "*bew*" of *fitz-bew* (Fig. 2C). Both *fitz-bews* and *fizz-bews* given with "two major throwbacks of the head" (Stein 1963: 24).

Also functions as an Advertising-Song vocalization; mixed in with *fitz-bews* and *fizz-bews* (Fig. 2D). Composed of several distinct notes, followed by a series of more closely spaced elements rising in frequency and amplitude (Stein 1963, JAS).

An upslurred note of simple structure (Fig. 2E); thick and dry, but softer than more

emphatic *whit* of Least Flycatcher; similar to calls of Dusky and Gray flycatchers, but easily told from Alder's low, flat *pip*, which sounds like a distant *Picoides* woodpecker, Hammond's Flycatcher (*E. hammondii*) *pip* call, or *kip* of Western Kingbird (*Tyrannus verticalis*; Lehman 1985, Whitney and Kaufman 1986, Sedgwick 1994). May be used in combination with other notes such as *writ-tus* (Fig. 2E).

This is the note Stein (1963) described as *pit* or *whit*. An upslur followed by a downslur (Fig. 2F); softer and more musical than *whit*, but also easily told from Alder's low, flat *pip* note. *Whups* sound like emphatic trill notes and often precede trill notes (Fig. 2F).

This is Stein's (1963) *Wee-oo* Call (Fig. 2E); begins with form of *whup* note, followed by a 150-ms terminal buzz; vaguely reminiscent of *fitz-bew* song. *Writ-tus* often preceded by *whits* (Fig. 2E) or trill notes (Stein 1963). Similar in Alder Flycatcher; Alder *pits* and *wee-oos* given together are similar to Willow *fitz-bew* (Stein 1963).

A rapid series of lower-intensity *whup* - like notes (Figs. 2F, 2G); this is Stein's (1963) *Churr* Call; often followed by a *writ-tu*.

Sound similar to *writ-tus* and vaguely like *fitz-bews* but somewhat buzzier (Fig. 2H); structurally resemble a *creet* followed by a descending *writ-tu* (compare Figs. 2D, 2E, and 2H); given infrequently in aggressive contexts.

Double-Peak Call. Allied to *whups* and *writ-tus*; 2 *whups* together or a *writ-tu* and a *whup*; rare in Willows but may occur in song series of Alders (Stein 1963).

Flight Song. A series of chase notes (*wheet*, *wheet*, *whee*) given in an increasingly rapid tempo, followed by a series (8–12) of *creets* and *fitz-bews*; given near dusk but not by all individuals on a given evening; flight songs begin shortly after sunset and continue until after dark (McCabe 1951).

Begging Calls. A raspy, low-pitched, 1-syllable call rendered as *cree*; given by older nestlings when begging for food from adults (JAS); presumably analogous to the *creet* -like notes

recorded in 16- to 20-d-old hand-reared birds by Kroodsma (1984).

Phenology

Singing most common shortly after arrival on breeding grounds and early in nesting cycle; singing declines as season progresses, but even in Aug, with fledged young, some males may sing intermittently throughout day (JAS). Unmated males sing at a higher intensity and longer into breeding season (Gorski 1969a, JAS) as do males with several territorial neighbors.

Mostly just calls (whit) on wintering grounds, but occasionally full song is given (Ridgely and Gwynne 1989, Ridgely and Tudor 1994, T. Koronkiewicz and M. Whitfield pers. comm.); will respond with song to tape playback on wintering grounds (Gorski 1969b). Some singing during northward migration (Sogge et al. 1997, JAS), but to what ex-tent is unknown. Stein (1963: 22) reports Advertising Song "used infrequently by migrating birds"; Graber et al. (1974) report that the "vast majority" of Empidonax (including Willow) do not sing during migration; in s. California, migrating Willow Flycatchers "rarely" sing (Unitt 1987) or "sing strongly" (M. Whitfield pers. comm.); apparently do so more frequently in n. California, possibly reflecting increasing hormone levels as birds approach breeding grounds (Unitt 1987). No records of song during autumn migration.

Daily Pattern

Male may sing throughout day, but frequency greatest in morning hours; often begins singing before dawn. Also often have a singing bout beginning after sunset and continuing for about 40 min (McCabe 1951, Weydemeyer 1973). Singing on wintering grounds, when it occurs, more common in early morning (M. Whitfield pers. comm.).

Places Of Vocalizing

Numerous perches in territory used for singing. Normally uses highest perches available (King 1955, Sedgwick and Knopf 1992, JAS).

Repertoire And Delivery Of Songs

Males (and presumably those females that do sing) sing 3 song types, *fitz-bew*, *fizz-bew*, and *creet*. (See Vocal array, above.)

Social Context And Presumed Functions

Chief functions of song presumed to be mate attraction, territory establishment, and territory defense. Whit and Whup calls appear to be used as alarm notes (JAS); whits also serve as a Contact Call between mates (Barlow and McGillivray 1983) and neighbors. Writ-tus are given in alarm contexts (Stein 1963, JAS); often accompanied by tail-flicking. Trill Calls presumably play a role in pair-bond establishment and maintenance, as they do in Dusky Flycatchers (Johnson 1963, Sedgwick 1993b; Fig. 2F); given in response to tape playback as well (Stein 1963, JAS), suggesting a territorial-defense function.

NONVOCAL SOUNDS

Bill-snapping, or the audible, rapid clicking of the mandibles, occurs in threatening contexts; common in other Empidonaces, as well (Gorski 1969a; Sedgwick 1993b, 1994).

Behavior

LOCOMOTION

Walking, Hopping, Climbing, Etc

Generally moves by flight; occasionally pounces on insects on ground.

Flight

Not described.

Swimming And Diving

Occasional in-flight bath-ing by diving to water surface. See Self-maintenance, below.

Self-Maintenance

Preening, Head-Scratching, Stretching, Bathing, Anting, Etc

Few detailed observations. Males preen and scratch head between singing bouts. Females observed preening on nest during incubation and brooding (JAS). Older nestlings do a great deal of preening, especially of wing- and tailfeathers. In-flight bathing by flying or diving from a perch to a water surface, immersing breast, and then returning to perch is not uncommon (JAS); after a bathing bout, individual shakes body and wings while perched, followed by preening and headscratching; process often repeated several times within a 1- to 2-min period (Burtt 1983, JAS).

Sleeping, Roosting, Sunbathing

Not reported.

Daily Time Budget

In Ontario, male Willow Flycatchers spent most of their available time sitting (i.e., perched; $62.6\% \pm 3.2$ SD) or singing (24.2% ± 3.8 SD); only small amounts of time foraging (4.9%), flying (4.3%), at the nest (3.5%), defending territory (0.3%), or in courtship (0.3%; 61 morning observation periods, 15 territories, over all breeding stages; Prescott and Middleton 1988). Willow Flycatchers thought to maintain a large component of uncommitted (sitting) time in order to minimize impact of short-term variations in competitor pres-sure and food supply.

AGONISTIC BEHAVIOR

In response to tape playback, 7 agonistic behaviors noted (listed in order of increasing aggressiveness; after Stein 1963):

Tail-Flick. Movement of rectrices in dorsoventral plane, given from 2/s to 1/10-15 s.

Crest-Raise. Erection of feathers on top of head; seen infrequently.

Spread. Extension or abduction of breast-feathers, making individual appear larger; tail held downward; crest-feathers sometimes raised as well.

Wing-Flick. Rapid extension and flexion of wing.

Tail-Flash. Lateral spreading and contracting of rectrices.

Supplant. Flying at another Willow Flycatcher causing it to fly off and then replacing it in position; associated with vocalizations and repeated.

Chase. Rapid flight of 2 individuals, accompanied by *churrs*.

These responses to tape playback were variable and strongest at beginning of breeding season; stronger in Willow than Alder flycatchers. Usually no response of Willow to Alder songs, of Alder to Willow songs, or of either species to songs of other Empidonaces. Thus, both Willows and Alders appear to be able to distinguish between *fitz-bews* and *fee-bee-os*.

Tail-pumping, crest-raising, billsnapping, and bill-wiping displacement observed in response to tape playback on wintering grounds; these displays plus gaping and breast plumage–fluffing used on breeding grounds to maintain territorial boundaries (Gorski 1969a).

SPACING

Territoriality

On breeding grounds, estimates of territory size vary: 4,071 m²± 1,092 SD (n = 12, nestling period only; Prescott 1986a); 3,000 m²± 2,000 SD (n = 8, egg or nestling period; Flett and Sanders 1987); averaged 0.70 ha in s. Michigan (range 0.32–1.17, n = 73; Walkinshaw 1966); 1.72 ha ± 0.35 SD in Colorado Rockies (Eckhardt 1979); 1.1–1.8 ha in New York (Stein 1958). Wintering birds appear to defend a specific foraging area; only 1 known estimate of wintering territory size: roughly 1,100 m², somewhat smaller than that on breeding grounds (Gorski 1969a, 1969b). In Ontario, territory size not strongly influenced by either competitor pressure or food availability; in addition, variation in territory size not attributed to constraints on feeding time, but was correlated with energy demands of all the territory's occupants (Prescott and Middleton 1988). Maintains territory larger than necessary to minimize impact of sudden changes in food availability and competitor pressure.

Individual Distance

No information.

SEXUAL BEHAVIOR

Mating System And Sex Ratio

Normally monogamous; sex ratio near 1:1, based on captures of adults (1988-1997) in se. Oregon (443 males:450 females) and returns of birds initially banded as (unknown sex) nestlings (114 males:100 females; Sedgwick and Klus 1997). Polygyny reported and not uncommon (Prescott 1986a, Sedgwick and Knopf 1989); as high as 15% in Oregon (JAS) and as high as 50% in some years in a small s. California population (Whitfield et al. 1998). Polygynous male typically divides his time between females and may or may not provide parental care at both nests (JAS). At 2 polygynous nests in Colorado, male made only 18% (n = 117; days 7, 12, 13, and 14 of nestling periods; 9.5 h observation) of all feedings (Sedgwick and Knopf 1989).

Pair Bond

Advertising Song important in pair-bond establishment and reinforcement; posture during song is upright, with head thrown back, tail flicked upward, and chest thrown outward. Advertising Song also likely an important component of territorial defense. Male may pursue female and then swoop down near her when perched, uttering a raspy, high-pitched " *wheak-dee-dee* " call, which is also thought to maintain pair bond (JAS).

Pairs and trios engage in vigorous sexual chase during courtship and territorial establishment (McCabe 1991). Territorial disputes among males frequent during prenesting, and intruding males may occasionally be attacked by both members of a territorial pair (King 1955). Physical contact rare; aggression usually consists of intricate pursuit flight and much calling by territory holder and invader (King 1955). Territorial fighting much less common beginning with egg-laying period (JAS).

High frequency of rematings in successive years. In se. Oregon (1988–1997), 27.1% of all pairings (n = 627) were with same mate; 29.5% (n = 325 returns) and 36.0% (n = 267 returns) of returning males and females, respectively, remated with a previous mate; 1 pair remained together for 5 consecutive years (JAS).

Extra-Pair Copulations

No observational evidence, but territorial intrusions common. Frequency of extra-pair paternity unknown but has been verified biochemically (Paxton et al. 1997).

SOCIAL AND INTERSPECIFIC BEHAVIOR

Degree Of Sociality

Solitary, maintaining intraspecific territories during breeding season.

Nonpredatory Interspecific Interactions

When sympatric with Alder Flycatcher, both species exclude the other from their territories (Prescott 1986b) but engage in territorial defense more frequently with members of their own species (Gorski 1969a). Competition not thought to be a strong selective force in maintaining interspecific territoriality in the genus Empidonax (Johnson 1963). Known for its aggressiveness to other bird species, especially near nest (Bent 1942, Gorski 1969a). Often observed attacking larger birds such as American Robins (Turdus migratorius) and Gray Catbirds (Dumatella carolinensis) when near nests with nestlings (Holcomb 1972a).

Despite similar habitat preferences of Alder and Willow flycatchers (s. Ontario), no evidence of competition generally observed (e.g., Barlow and McGillivray 1983); Prescott (1987b), however, found that both species

aggressively responded to song playback of the other species in shared habitats and suggested that both learn through coexistence to recognize the other's song as that of a potential competitor; aggressive response to heterospecific song in allopatric populations is practically absent. In areas of sympatry, both species vigorously excluded the other from their territories (Prescott 1986b) but engaged in territorial defense more frequently with members of their own species (Gorski 1969a). Male Willow Flycatchers always more dominant in cases of contact with Alders (Gorski 1969a), and Alders can be displaced by the more aggressive Willow Flycatcher (Prescott 1987b). Unrelated adults, likely either floaters or adults of failed nests, rarely help parent Willow Fly-catchers feed their fledglings; 1 instance of a Dusky Flycatcher feeding Willow Flycatcher fledglings (Stafford 1986).

PREDATION

Few data. McCabe (1991) reported finding Willow Flycatcher eggs in the stomach of a milk snake (Lampropeltis triangulum) that had been harassed by a pair of Willows. Common king snake (L. getula), Cooper's Hawk (Accipiter cooperi; e.g., Paxton et al. 1997), and Great Horned Owl (Bubo virginianus; Stoleson and Finch 1999) known nest predators. In British squirrels Columbia. red (Tamiasciurus hudsonicus) and striped skunks (Mephitis mephitis) observed or suspected nest predators of 45% and 15%, respectively, of 60 nests; other predators included House Wren (Troglodytes aedon), chipmunk (Tamias spp.), northern flying squirrel (Glaucomys sabrinus), Common Raven (Corvus corax), Clark's Nutcracker (Nucifraga columbiana). American Crow (Corvus brachyrhynchos), black bear (Ursus americanus), Steller's Jay (Cvanocitta stelleri), and domestic dog (Canis familiarus; Campbell et al. 1997); ring-tailed cat (Bassariscus astutus), fox (Vulpes spp.), and domestic cat (Felis domesticus) other suspected predators. In se. Oregon, most nest predation believed to be mammalian, including long-tailed weasel (Mustela frenata), mink (M. vison), and voles (Microtus spp.; JAS). Mule deer (Odocoileus *hemionus*) trample some low, fragile nests in cow parsnip (*Heracleum lanatum*) in Oregon. In areas where grazing occurs, cattle may knock over nests as they move through shrubby vegetation (King 1955, Valentine et al. 1988). No information on response to predators.

Breeding

PHENOLOGY

Pair Formation

No information.



Figure 3. Annual cycle of breeding, molt, and migration of the Willow Flycatcher

Nest-Building

In Ohio and Nebraska, earliest first nests in 4 yr were 7 Jun, 22 May, 2 Jun, and 2 Jun (Holcomb 1972a). Begins early to mid-Jun in Oregon and Colorado, mid- to late May farther south (s. California, s. Arizona).

First/Only Brood Per Season

See Figure 3. Earliest and latest dates for full clutches in Washington: 25 May and 13 Jul (Jewett et al. 1953), and 19 Jun and 24 Jul (King 1955). In Wisconsin, McCabe (1991) reported

mean first egg, hatching, and fledging dates as 27 Jun, 12 Jul, and 25 Jul, respectively. Mean first egg date in s. Michigan 17 Jun (earliest 11 Jun) and mean nest termination 19 Jul (latest 14 Aug; n = 23 females; Walkinshaw 1966). In n. Sierra Nevada, earliest and latest fledging dates 21 Jul and 2 Sep, respectively (H. Bombay pers. comm.); in s. Sierra Nevada, earliest and latest egg dates 25 May and 29 Jul, and earliest and latest fledge dates 26 Jun and 27 Aug (M. Whitfield pers. comm.). For first nests in se. Oregon, mean first egg date 22 Jun (median 22 Jun, range 5–30 Jun, n = 439 nests) and mean fledging date 21 Jul (median 22 Jul, range 5 Jul-8 Aug. n = 572; JAS). Late renest clutches in se. Oregon may not fledge until mid-Aug (latest 26 Aug; JAS). Dates for 63 broods in British Columbia from 13 Jun to 25 Aug (Campbell et al. 1997).

NEST SITE

Selection Process

Female selects site, collects nest material, and builds nest while male perches nearby (Gorski 1969a, JAS). Female may use materials from previously used (failed) nests of the season, often using all of the old nest to construct the renest (JAS). Renest site is within territory close to original nest site (mean 27.4 m, n = 25 renestings; McCabe 1991); occasionally in same bush (JAS).

Microhabitat/Site Characteristics

Low in crotch of bush or small tree near water (Hoffmann 1927); close to ground in low shrubs and bushes (Jewett et al. 1953) but generally placed higher in bush than Alder Flycatcher nests (Walkinshaw 1966, Campbell et al. 1997); nests at outer edge of shrub or thicket and near edges of shrub clumps, thus easily approached (Berger and Parmalee 1952, King 1955, Johnsgard 1979, Valentine et al. 1988). Across its range, willow shrubs are a frequently selected nesting substrate, but many other species of shrubs, and occasionally trees are used, five-stamen tamarisk including (Tamarix chinensis; Southwest), box elder (Acer negundo; sw. New Mexico), coast live oak (Quercus agrifolia; s. California), elder (Sambucus spp.) and red-osier dogwood (Cornus stolonifera; Wisconsin).

In Michigan, nests in both dense thickets isolated bushes, including dogwood, and Crataegus (hawthorn), willow, Cephalanthus (buttonbush), elder, Alnus (alder), Pyrus (pear), Ligustrum (privet), and Lonicera (honeysuckle; Berger and Parmalee 1952); in s. Michigan majority of nests in dogwood spp. (48%), willow sp. (15%), hawthorn sp. (9%), and American elder (Sambucus canadensis; 12%; n = 93; Walkinshaw 1966); in Illinois, most nests (Traill's Flycatcher) in Osage orange (Maclura *pomifera*: 47.9%) and willow (13.6%; n = 73; Graber et al. 1974); in Ohio, most nests in grav dogwood (Cornus racemosa), hawthorn spp., and willow spp. (Holcomb 1972a); in Wisconsin, elder and red-osier dogwood accounted for 84% (n = 619 bushes) of nestbush sites (McCabe 1991). Salix principal nesting shrub genus in New York (Stein 1963). In interior British Columbia, most nests in rose (56%) and willow (13%; n = 147); on coast, most in bracken fern (Pteridium aquilinum; 43%) and rose (18%; n = 44; Campbell et al. 1997). Bracken fern also a common substrate in w. Washington (Bent 1942). In Palouse Hills of Washington, most nests in rose, hawthorn, cow parsnip, and chokecherry (King 1955). In se. Oregon (Malheur NWR), >90% of nests (n =1,168) in willow shrubs, with most of remainder in rose and cow parsnip (JAS). In sw. New Mexico (1997-1999), most nests in box elder (74.4%) and willows (11.9%); n = 403; S. Stoleson pers. comm.). In s. California, most in willow (73%), nettle (Urtica; 9%), or a combination (14%; n = 332; Whitfield et al. 1998).

In Michigan, mean nest height 1.3 m (range 0.6–2.8 m, n = 93 nests; Walkinshaw 1966). In Ohio and Nebraska, mean height of 1.4 m (range 0.73–2.78 m, n = 80; Holcomb 1972a); in Wisconsin, 1.4 m \pm 0.02 SE (n = 619; McCabe 1991). In British Columbia, nest height 0.6–20.0 m (n = 187), with 73% between 0.9 and 1.5 m; generally placed higher in bush than Alder Flycatcher nests (Walkinshaw 1966, Campbell et al. 1997). In se. Washington 83% of nests (n = 41) between 0.51 and 1.02 m above the ground (King 1955). In s. California, mean nest height 2.39 m \pm 0.13 SE (n = 205; Whitfield

et al. 1998). A population of *E. t. extimus* in sw. New Mexico nesting largely in box elder placed nests much higher than in other populations of Willow Flycatcher: mean height 7.5 m \pm 3.7 SD (range 1.0–19.5, n = 374 nests; S. Stoleson and D. Finch pers. comm.).

See also Habitat, above.

NEST

Construction Process

Female builds nest (Gorski 1969a, McCabe 1991). Four stages of nest-building, according to King (1955: 156): (1) begins with a platform of grass and decayed weed bark or other soft strips of vegetation; (2) a cradle is woven upon the foundation and to supporting twigs to anchor nest; (3) additional loose material is placed in cradle until there is sufficient mass to support nest cup; (4) dry grass stems are laid and turned to form cup and rim, "using the mandible like a trowel" and turn-ing in the nest cup to shape it to bird's body. Nest framework tied to supporting branches, with additional foundation material added to nest bottom, weaving and tying in vegetable fibers. Wiry rootlets, stiff grass stems, horsehair, or other finer materials added as nestlining. Nest may include a few wads of plant floss and feathers. Inserting materials into nest and nest rim, wrapping nest material around nest-crotch branches, pecking at nest rim, and molding inner cup with breast are typical nestbuilding behaviors (JAS). In se. Oregon, females frequently seen hovering at dead willow or old stinging nettle (Urtica dioica) stems, attempting to pull off and collect shreds of nesting material (JAS).

Total construction time probably varies with motivational state: Gorski (1969a) reported about 36 h to complete a nest versus about 5–7 d (n = 4 nests; Bent 1942) and 7–10 d for initial nesting attempts (McCabe 1991). Renests constructed in less time: 4.2 d (n = 25; Holcomb 1974); 4.7 d (n = 23; McCabe 1991). At 2 nests observed during construction for a total of 16.5 h, individuals arrived at nests every 7.3 and 10.0 min, 57% of time with material (McCabe 1991).

Structure And Composition Matter

Woven of weed stems, plant fibers, pine (Pinus)



Willow Flycatcher nest, California

needles, shreds of bark, and dry grasses; lined with feathers, hair, rootlets, and finer materials (Hoffmann 1927, Jewett et al. 1953). Outside of nest may contain lichens, paper, cocoons, and shredded grass; lining may include fine grass, lichens, and cottony material (Stein 1963). Cottony materials from old thistles (*Cirsium*) and stems of swamp milkweed (*Asclepias incarnata*), fur, feathers, and deer hair used in Michigan (Walkinshaw 1966); primary material for outer shell in Ohio nests was swamp milkweed (Holcomb 1972a); primary materials in se. Oregon shredded willow bark and shreds of old stinging nettle stems (JAS).

Nest usually more compact, less ragged than that of Alder Flycatcher (Aldrich 1953, Stein 1963, Zink and Fall 1981); similar to nest of Yellow Warbler (Dendroica petechia), whereas Alder nest suggests that of bush-nesting Song Sparrow (Melospiza melodia). Nest often has gravish appearance, often with cottony materials on outside of cup; some nests with streamers dangling from nest base (more common in Alder nests; Snyder 1953, Stein 1963, Gorski 1969a, Campbell et al. 1997). Many nests have characteristic "tangential protrusion" of ends of grass stems in nest rim (King 1955, JAS). Alder Flycatcher nests are generally less compact, have few feathers, little cottony material, and often have streamers at bottom of nest (Stein 1963). Willow Flycatcher nests that are not in upright forks are often of looser construction and generally show wider structural variation than Alder nests do (Stein 1963).

Dimensions

In s. Michigan (n = 24), as follows: outside diameter, mean 8.2 cm (range 7.1-9.9); outside height, mean 6.7 cm (range 5.4–10.5); inside cup diameter, mean 5.2 cm (range 4.7-5.7); inside cup depth, mean 3.9 cm (range 3.1-4.6; Walkinshaw 1966). In Ohio and Nebraska, mean nest dimensions (n = 66) were: outside diameter 7.7 cm \pm 0.1 SE, outside height 7.2 cm \pm 0.1 SE, inside cup diameter 5.3 cm \pm 0.1 SE, and inside cup depth 3.8 cm \pm 0.0 SE (Holcomb 1972a). additional nest See Stein (1958) for measurements. Nest weight: 6.9 g (range 3.3-12.1, n = 18; after use; Walkinshaw 1966); and, 8.7 g (n = 155, dried at room temperature; McCabe 1991).

Microclimate

Nest's microclimate and insulation more than compensate for heat loss through brood patch; even after accounting for heat required to raise temperature of eggs after female has been off of nest foraging, the energy expenditure of incubating females averaged 11% below that of nonincubating birds (Walsberg and King 1978). As McCabe (1991: 64) put it: Nest-molding and bowl-shaping by female during construction creates an ideal incubator, and female "fills the nest opening as snugly as the lid on a teapot."

Maintenance Or Reuse Of Nests, Alternate Nests

Most nests used only once and not actively main-tained once built; a few cases of nest reuse docu-mented in California and Arizona (Whitfield 1990, Yard and Brown 1999). Females often completely remove nesting material from first nests to use in construction of replacement nests following pre-dation or abandonment (Holcomb 1972a, JAS). McCabe (1963) demonstrated this when yarn woven into first nests, from which eggs were experimentally removed, was transferred to and found in replacement nests. In se. Oregon, a mean of 1.49 \pm 0.02 SE nests built/season/female (n = 782

females; Sedgwick and Iko 1999). No records of alternate nests.

Nonbreeding Nests

None reported.

EGGS

Shape

Ovate, elliptical-ovate, or short-ovate.



Willow Flycatcher clutch, Oregon

Size

Mean length × width: 17.70 mm (range 15.2– 19.3) × 13.29 mm (range 12.5–14.3, n = 155; Walkinshaw 1966); 17.98 mm ± 0.06 SE × 13.72 mm ± 0.04 SE (n = 164; Holcomb 1972a). Mean length × width for 21 clutches (78 eggs) from collection of the Western Foundation of Vertebrate Zoology (WFVZ): 18.15 mm (range 17.03–20.08) × 13.64 mm (range 13.07–14.26). This compares with 50 eggs reported in Bent 1942, averaging 17.8 × 13.3 mm. Eggs having extreme lengths and widths meas-ured 19.3 × 13.7, 18.8 × 14.7, 15.5 × 12.7, and 16.3 × 12.4 mm. See Stein 1958 for additional egg measurements.

Mass

Mean fresh egg mass: 1.7 g (n = 168 eggs); no difference in egg mass according to sequence of egg laid (Holcomb 1972a, 1974); 1.67 g (n = 83; Walkinshaw 1966).

Color

Creamy white or buff; dotted, blotched with brownish to blackish irregular spots about large end, often in a loose wreath (Hoffmann 1927, Jewett et al. 1953, Walkinshaw 1966, JAS); unspotted eggs not uncommon (Brewer 1879, JAS). Eggs of Alder Flycatcher whitish with more defined, smaller spots (Stein 1963).

Surface Texture

Smooth, little or no gloss.

Eggshell Thickness

No data. Empty shell weight: 0.083 g, range 0.071-0.091 g (n = 78 eggs; WFVZ).

Volume

Mean volume 1.4 ml \pm 0.168 SD (n = 55); maximum difference in volume within a 4-egg clutch 0.2 ml (McCabe 1991).

Clutch Size

Usually 3 or 4 eggs, occasionally 5 (JAS). Clutches in Southwest possibly smaller; renest clutches smaller (Holcomb 1974, McCabe 1991, JAS). See Demography and populations: measures of breeding activity, below.

Egg-Laying

One egg/d; often 1 day is skipped, so 4-egg clutch complete in 5 d. Eggs usually laid in morning, but some in early afternoon (JAS); at 5 nests in se. Oregon where laying was followed closely (nests checked at hourly intervals beginning at 06:30 PDT), third eggs were laid between 07:29 and 08:31, 08:44 and 09:45, 08:47 and 09:48, and 08:51 and 09:53, and one fourth egg between 10:39 and 11:39 (JAS). Holcomb (1972a) found that most eggs were laid before 09:30, but 1 was laid after 11:00. Mean of 6.6 d (n = 18 renests; Holcomb 1974) and 6.5 d

(n = 21 renests; McCabe 1991) between first nest loss and initial egg-laying in renest.

INCUBATION

Onset Of Broodiness And Incubation In Relation To Laying

Some irregular daytime sitting occurs before clutch is complete (JAS). Unknown at what stage of egg-laying female begins sitting on eggs continuously at night. Given that eggs hatch over a 1- to 3-d interval (McCabe 1991, JAS), eggs must be maintained for periods long enough for embryonic growth prior to laying of last egg, perhaps similar to incubation behavior in Dusky Flycatcher (Morton and Pereyra 1985; Sedgwick 1993a, 1993b).

Incubation Patch

Females have brood patch; males have none (Pyle 1997a, JAS, but see Gorski 1969a and below).

Incubation Period

In Wisconsin, 14.8 d (n = 50; McCabe 1991); in Nebraska and Ohio, 13.3 d ± 0.1 SE (range 12– 14, n = 28 nests; Holcomb 1972a); in s. Michigan, incubation periods were 15 d at 3 nests, 14 d at 3 nests, and 13 d at 1 nest (from last egg laid to last or all eggs hatched; Walkinshaw 1966).

Parental Behavior

Female generally performs all incubation duties (McCabe 1963, 1991; JAS). This seems to be the rule for Tyrannidae (Nice 1943, Skutch 1957). Most authors agree, but 1 report (Gorski 1969a) of occasional incubation by males, 2 of which had thickened, vascularized brood patches; based on limited observations, incubation by males most common in afternoon, when female is off the nest foraging.

Female sits low in nest during incubation, body horizontal, head and tail up at an angle of about 45°; occasionally closes eyes for brief intervals and lets head and tail droop over side of nest (JAS). Standing on rim and shading eggs not uncommon (JAS). Eggs checked and turned periodically; female

typically rises and backs up in nest, puts head down in nest cup and apparently turns eggs with vigorous head movements. Foot movement also used when bird is incubating; whole body quivers as feet are used to move and turn eggs, similar to behavior in other flycatchers (Sedgwick 1993a, 1993b).

In Ohio, 2 females observed during 34.9 h of incubation were in attendance 64.0% of the time, less during days 1–4 of incubation (57.3%) than during days 5–8 (73.5%) or days 9–13 (64.8%; Holcomb 1972b); mean attentive and inattentive bouts averaged 10.1 and 5.7 min, respectively. Behaviors of female during incubation (preening, turning, standing, and adjusting eggs, spreading wings, shutting eyes, settling movements) similar to those reported for other *Empidonax* (Holcomb 1972b; Sedgwick 1993a, 1993b, 1994).

Hardiness Of Eggs Against Temperature Stress; Effect Of Egg Neglect

Not reported. Of 1,442 eggs in complete clutches, 42 (2.9%) were infertile or addled (McCabe 1991).

HATCHING

Preliminary Events And Vocalizations

Voice just after hatching is a faint *weep-weep-weep*, uttered without opening bill (King 1955).

Shell-Breaking And Emergence

Brood hatches over a period of 1-3 d; in Wisconsin, eggs hatched in 1-2 d in 90% of 160 clutches, and in 3 d in the remainder (McCabe 1991).

Parental Assistance And Disposal Of Eggshells

Eggshells removed by female and dropped at some distance from nest (McCabe 1991, JAS).

YOUNG BIRDS

Condition At Hatching

Altricial, nidicolous, eyes closed, and naked except for tufts of down on crown, spinal, alar, humeral, and femoral tracts; flesh-colored skin (Walkinshaw 1966). White-tipped egg tooth visible until 4–5 d after hatch; via heterogonic growth, it rotates from its initial position on the culmen, and at about 12 d appears as a minute tubercle on the hook of the bill (King 1955).

Growth And Development

From King (1955), based on n = 2-9 nestlings.

Newly Hatched. Birds rest on huge belly and crown of turned-under head; gaping response appears 12 h after hatching; much down on crown, tufts on spinal and alar tracts; 3 or 4 down feathers on humeral, femoral, and crural tracts; about 7 down feathers on each side of abdominal portion of ventral tract; remigial papillae visible as minute blue-black dots; only motor response a pedaling motion of legs and toe movement; voice a faint *weep-weep* without opening bill.

Day 1. Papillae of contour feathers visible in cervical region of ventral tract in some individuals.

Day 2. Dark papillae visible in all feather tracts; sheaths of secondaries distending skin or barely projecting through skin.

Day 3. Contour feathers of pectoral region piercing skin; sheaths of spinal and humeral tracts beginning to pierce skin; sheaths of primaries <1 mm through skin.

Day 5. Pin-feather stage; sheaths much elongated, but rupturing only in pectoral and abdominal regions; sheaths of rectrices <1 mm through skin; median length of tenth primary sheath 4.6 mm.

Day 6. Eyes begin to open; wings first used in strong fluttering motions.

Day 7. Vanes of contour feathers well expanded except in frontal, gular, auricular, malar, and submalar regions; secondary vanes expanded ≤ 1 mm; sheaths of first and second primaries beginning to rupture; vanes of inner rectrices expanded 1 mm; median length of tenth primary 10.4 mm. **Day 8**. All remigial sheaths ruptured; growth of contour feathers substantially ended; median length of tenth primary and vane 13.4 mm; nestling more active, able to manipulate and fold wings; glances about alertly.

Day 9. Wing-bars well defined; ventral apterium still exposed but dorsal and lateral apteria covered by converging contour feathers when nestling is in repose; median length of tenth primary 16.2 mm.

Day 10. Well feathered except for frontal, auricular, gular, malar, and submalar areas where sheaths still prominent; upper wingcoverts cover or nearly cover unruptured portion of remigial sheaths; median length of 10th primary 18.8 mm.

Days 11–13. Ventral apterium covered by converging feathers of ventral tract; endysis complete in head region by day 12; fledging may occur on day 12 or 13.

From Walkinshaw 1966. In Michigan, body mass (mean): day 0 (hatching day), 1.28 g (range 1.2–1.4, n = 7); day 1, 2.57 g (range 1.6– 3.3, n = 7); day 3, 4.2 g (range 3.0–5.7, n = 7); day 7, 8.1 g (range 8.0–8.4, n = 6); day 10, 11.5 g (n = 7); day 11, 11.7 g (range 10.1–13.4, n =3).

From King 1955. In Washington, median weights: day 0, 1.8 g; day 1, 2.5 g; day 2, 4.0 g; day 3, 5.5 g; day 4, 7.2 g; day 5, 8.9 g; day 6, 10.3 g; day 7, 11.5 g; day 8, 12.9 g; day 9, 13.5 g; day 10, 14.3 g; day 11, 15.0 g; day 12, 14.1 g; day 13, 13.3 g (n = 2-9 nestlings, 3 nests).

Daily rate of growth starts low (0.6 g/d), peaks at about 5 d of age (1.37 g/d), then decreases (0.22 g/d by day 12); percentage of increase in weight/d is highest at day 0 (37%) and decreases through nestling phase (15%/d on day 5, 2%/d on day 12; McCabe 1991).

PARENTAL CARE

Brooding

Mostly by female, but McCabe (1991) observed some exchanges of brooding adults at nest; male's role believed to be minor. During early brooding phase, posture of brooding female similar to that of incubating female; i.e., low in nest, covering nestlings. Brooding most common from 1 to 5 d, then decreases, and daytime brooding ceases beginning about 6–7 d after hatching (JAS). Brooding, including standing on rim and shading young with outspread wings, increases during periods of high temperature (McCabe 1991) and during cool, wet periods (JAS). Males may (rarely) feed females on nest during brooding (M. Whitfield pers. comm., JAS).

Feeding

Both adults feed young, but female plays major role (Holcomb 1972a, McCabe 1991, JAS). In Washington, male visits nest only about 0.75 times as frequently as does female (Ettinger and King 1980); 17.9% of feeding trips by male at 2 polygynous nests in Colorado (Sedgwick and Knopf 1989). In Oregon (1993), at 3 different nests where both adults were color-banded (n =22 h observation, 454 feeding trips, nestlings ranging from 4 to 14 d of age), females and males fed 59.3% and 3.7% of the time, respectively; remainder of feedings were by an individual of undetermined gender (JAS). Biparental care of nestlings in Willow Flycatchers may not be essential to reproductive success, especially in the kinds of highly productive environ-ments they normally inhabit.

Flight to nest with food typically direct, either to nest or to twig near nest. Before age of 5–6 d, nest-lings appear unaware of incipient feeding, but after that time seem to anticipate arrival of an adult with food by exhibiting excited behavior and Begging Calls (JAS). Food inserted into mouth of nestlings when they gape. Adults usually silent during feeding trips.

Feeding rate of nestlings in Wisconsin was 22.2 trips with food/h/nest (n = 1 nest, 395 feeding trips, 17.8 h observation, 3 nestlings; McCabe 1991). Feeding rate increased from day 1 to day 7, then declined somewhat until fledging; time between trips with food decreased and then increased accordingly (McCabe 1991). In se. Oregon, feeding rate was 20.6 trips/h/nest (n = 3 nests, 454 feeding trips, 22 h observation, 1–3 nestlings/nest, 4–14 d of age; JAS). In s. California, feeding rate (both adults) increased from 3.23 feedings/h/nestling ± 0.12 SE to 5.29 ± 0.15 SE and 7.58 ± 0.13 SE for 3- to 5-, 5- to 8-, and 9- to 12-d-old nestlings, respectively (n =13 nests, 119 h observation; some males polygynous; M. Whitfield pers. comm.).

Nest Sanitation

Adults nearly always remove fecal sacs produced by nestlings. Adults remain on nest rim in a watching attitude after feeding a nestling and grasp fecal sac as it exits vent of nest-ling. Adults may gently probe cloacal region of nestling with bill in apparent attempt to stimulate defecation (McCabe 1991, JAS). Most fecal sacs carried off and dropped some distance from nest; a small proportion eaten by adults, most often early in nestling phase (JAS). Near fledging, a small percentage of feces may not be removed. In Wisconsin, McCabe (1991) recorded a nestling defecation rate/nest of 3.1/h (n = 1 nest, 17.8 h observation, 3 nestlings).

COOPERATIVE BREEDING

Not known to occur.

BROOD PARASITISM

Identity Of Parasitic Species

Brown-headed Cowbird (Molothrus ater).

Frequency Of Occurrence, Seasonal Or Geographic Variation

Highly variable, both temporally and geographically. Parasitism by cowbirds in e. U.S. averaged 11% (6 studies, n = 859 nests; includes some Alder Flycatchers; Friedmann 1963). Only 8% of 88 nests parasitized in a Nebraska and Ohio study (Holcomb 1972a); Walkinshaw (1961, 1966) reported a parasitism rate of only 7.5% (4/53 nests) and 5.3% (5/94 nests) in Michigan (may include Alder Flycatcher); Berger (1967) reported a parasitism rate of 10.1% (33/325 nests, Michigan). In Wisconsin, 9.3% of 537 nests parasitized (McCabe 1991).

Western populations once thought to experience only about half the parasitism of

eastern populations (Friedmann et al. 1977; may include some Alder in analysis) but Hanna (1928) found Willow Flycatchers to be among the most heavily parasitized species in s. California in 1920s. Sedgwick and Knopf (1988) reported that 40.7% of nests (n = 27) and >73% of pairs (n = 15) were parasitized in Colorado; in Oregon (1988–1997), parasitism rate of Willow Flycatcher pairs (n = 882) averaged 23.4%, ranging from 10.9 to 40.7% over 10 yr (all study areas combined) and from 15.4 to 41.5% across 3 different study areas (all years combined; Sedgwick and Iko 1999). In British Columbia, 36% of 210 nests parasitized (Campbell et al. 1997). In s. California, nest parasitism was 63% (n = 116 nests; 1989-1991; Whitfield et al.1999); in sw. New Mexico (1997-1999), 35/178 (19.7%) nests parasitized (S. Stoleson and D. Finch pers. comm). See also Berger and Parmalee 1952, King 1955, and Harris 1991.

Timing Of Laying In Relation To Host's Laying

Cowbirds generally lay the day before first Willow Flycatcher egg is laid or on the day the first or second egg is laid (JAS).

Response To Parasitic Mother, Eggs, Or Nestlings

Only 1 instance of "flooring" over or building a new nest-lining over cowbird egg(s) reported by Friedmann (1963), a behavior now known to be common (Sedgwick and Knopf 1988, McCabe 1991, JAS). Flycatchers do not remove cowbird eggs (Sedgwick and Knopf 1988), but will bury eggs into nest lining or abandon nest if cowbird eggs laid too early in flycatcher's nesting cycle; nest may then be dismantled and nesting material reused in construction of a renest (Sedgwick and Knopf 1988, Whitfield 1990). On rare occasions, flycatchers may respond to parasitism by building a complete second nest on top of parasitized one (M. Whitfield pers. comm., JAS). Because Willow Flycatchers are late nesters, many second and later (re)nests infre-quently parasitized as they occur after main period of cowbird parasitic activity (Sedgwick and Knopf 1988). Inconspicuous behavior near nest appears to be adaptive as cowbird parasitism was associated with noisier

flycatcher pairs in a California study (Uyehara and Narins 1995).

Effects Of Parasitism On Host

After Sedgwick and Iko (1999). In Oregon (1988-1997; n = 882 pairs), nest success (pairs) fledging ≥ 1 young) of parasitized pairs was 50.3% less than that of unparasitized pairs. Parasitized pairs had fewer eggs survive to fledging (17.3 versus 51.4%), lost more eggs (3.08 versus 1.28) and more nestlings (1.18 versus 0.79), and reared fewer offspring (0.80 versus 2.11) in a season compared to unparasitized pairs. Parasitized females also incurred higher costs by spending more time attending nests (2-4.5 d), building more nests (1.83 versus 1.38), laying more eggs (4.72 versus 4.12), and fledging young later (4 d) within a season compared to unparasitized females.

Return rates and survival varied by age and sex: Although there was no difference in the overall return rates or survival of parasitized versus unparasitized females, or of their young, males of parasitized pairs tended to survive longer than unparasitized males (1.29 versus 1.01 yr). Among successful pairs, return rate of females parasitized in their initial year of capture was greater than that of unparasitized females, but survival did not differ between these groups. There were no differences in return rates and survival between parasitized and unparasitized successful males. Lifetime reproductive success of females depended on their parasitism and first-year success status: Parasitized females reared significantly fewer young over their life spans than unparasitized females (2.25 versus 4.09 young), but there was no difference in lifetime output between these groups in years subsequent to their first breeding season (2.84 versus 3.49 young). Whether females were successful or not, or parasitized or not, did not significantly affect re-productive success in subsequent years. Seasonal-fecundity losses due to predation (0.74 young/pair) were greater than losses to parasitism (0.30 young/pair); lifetime reproductive losses displayed similar trends (predation versus parasitism losses: 0.70 young/pair versus 0.37 young/pair).

In s. California, parasitized nests of *E. t.* extimus had a lower hatching rate (20 versus 61%; n = 281 nests), fledging rate (11 versus 47%; n = 281 nests), and nest success (14 versus 54%; n = 323 nests) than unparasitized nests (1989–1997); in Arizona, nest success was 13% and 60% at parasitized and unparasitized nests, respectively (n = 164 nests; Whitfield and Sogge 1999).

Success Of Parasite With This Host

In se. Oregon (1988-1997), 23.5% of 204 parasitized Willow Flycatcher pairs produced a cowbird: 8.8% fledged both a cowbird and flycatcher(s), 27.9% fledged only flycatchers, and 39.7% failed to produce any fledglings (Sedgwick and Iko 1999). More parasitized flycatcher pairs (n = 75) fledged flycatchers than fledged cowbirds (n = 66); flycatchers raised 0.32 cowbirds/parasitized pair. Success of parasite versus host was reversed on a per-nest basis in Arizona (1992-1996) and California (1989-1997; Whitfield and Sogge 1999). In Arizona, 30% of parasitized nests (n = 40)fledged a cowbird and only 7.5% fledged a Willow Flycatcher; in California (cowbird trapping/removal in 6 of 9 yr), 14% of parasitized nests (n = 72) fledged a cowbird, 1.4% fledged both, and only 9.7% fledged a flycatcher.

FLEDGLING STAGE

Departure From Nest

Nestling period 14–15 d (Berger and Hofslund 1950, McCabe 1991). Berger (1967) reported 13–16 d for 45 young. Five family groups in s. Michigan fledged after an average of 13.8 d in nest (n = 13 young; Walkinshaw 1966); in a Nebraska and Ohio study, 82 young fledged between 11 and 14 d (mean 12.3 d ± 0.1 SE; Holcomb 1972a). Nestlings may move some distance from nest for short intervals during fledging process, only to return to nest (McCabe 1991, JAS).

Growth

No information once young leave nest.

Association With Parents Or Other Young

The first few days after fledging, fledglings often huddle together on same perch; remain near nest for 3–4 d, and then follow adults through territory until 24–25 d old (Walkinshaw 1966). In se. Oregon, fledglings remain on parents' territory about 14 d and then disperse (JAS).

Ability To Get Around, Feed, And Care For Self

Young unable to fly at 12 d of age but can make short flights (30 m) at 14 d. Adults observed feeding young until dispersal from territory (JAS).

IMMATURE STAGE

Broods probably break up once fledglings leave parents' territories; flocking of immatures not reported.

Demography and Populations

MEASURES OF BREEDING ACTIVITY

Age At First Breeding; Intervals Between Breeding

First breeds as 1-yr-old and annually thereafter.

Clutch

Mean of 3.68 ± 0.1 SE for first nests (n = 31) and 3.14 \pm 0.1 SE for renests (n = 29) in Nebraska (Holcomb 1974). In Wisconsin, McCabe (1991) reported a mean clutch size of 3.59 ± 0.49 SD (*n* = 415 clutches), with 58% of clutches being 4 eggs; early (before 28 Jun) clutches (mean 3.68, n = 243) larger (p < 0.001) than late clutches (mean 3.49, n = 172), and first clutches (mean 3.5) larger than renest clutches (mean 3.2) for the same pairs (n = 21). In se. (1988 - 1997),first Oregon mean nest (unparasitized) clutch size 3.69 ± 0.03 SE (range 1-5, n = 365 clutches); 69.6% were 4 eggs and 26.9% were 3 eggs (JAS). In s. California (E. t.

extimus) first, second, and third clutch sizes: 3.63 ± 0.05 SE (n = 113), 2.90 ± 0.09 SE (n = 50) and 2.71 ± 0.19 SE (n = 14), respectively (M. Whitfield pers. comm.). In s. New Mexico, mean clutch size reported as 3.06 ± 0.63 SE (n = 50; includes second and later nestings; S. Stoleson pers. comm.). *E. t. extimus* first nests in Arizona (1996–1999, unparasitized nests only) had average clutch of 2.92 ± 0.73 SD (n = 321; T. McCarthey pers. comm.).

Renests thought to have fewer eggs primarily because of short interval between firstnest destruction and renesting, which leaves inadequate time for building energy reserves to lay a full clutch of eggs; thus second clutches laid rapidly at the ex-pense of laying fewer eggs, presumably so that second nesting is not out of phase with optimal conditions for feeding and survival of young (Holcomb 1974, McCabe 1991).

Annual And Lifetime Reproductive Success

Nest success (nests producing ≥ 1 fledgling) variable. In Wisconsin, 315 of 459 nests (68.6%) were successful, 72.4% of eggs (n = 1,598)hatched, 84.6% of nestlings (n = 1,157) fledged, and 2.13 young fledged/nest (McCabe 1991); the Mayfield method (Mayfield 1961, 1975) yielded more modest nest success of 51% (McCabe 1991). In British Columbia, nest success 28% (n = 96 nests; Campbell et al. 1997); much higher in s. Michigan, where 65.2% of 92 nests fledged young, 73.8% of 302 eggs hatched, and 65.6% of eggs resulted in fledglings (or 2.15 fledglings/nest; Walkinshaw 1966). In Ohio and Nebraska, Holcomb (1972b) reported 39.5% nest success (n = 91 nests), 1.11 young fledged/nest, and 1.41 young/pair for 29 closely watched pairs; 1 female followed for 6 yr laid at least 20 eggs and fledged 13 young. In Washington, 63 of 68 (92.6%) eggs hatched and 21 of 47 (44.7%) nestlings successfully fledged (King 1955). In sw. New Mexico (1997-1999), 43.3% of 298 nests fledged ≥ 1 young (S. Stoleson and D. Finch pers. comm.), and in Sierra Nevada, 60% (*n* = 25) and 50% (*n* = 64) of nests fledged ≥ 1 young in 1997 and 1998, respectively (H. Bombay pers. comm.).

After Sedgwick and Iko 1999. In a 10-yr study in se. Oregon, 60.2% of 3,537 eggs hatched and 42.7% survived to fledging; 70.9%

of 2,131 eggs surviving to the nestling phase resulted in fledglings. Pair success (pairs producing ≥ 1 fledgling) was 65.4% (n = 875pairs). Seasonal fecundity: mean of 4.26 ± 0.05 SE eggs laid/season/female (n = 831females); 1.81 ± 0.05 SE young fledged/female (n = 874 females), with fecundity reduced by a loss of 1.69 ± 0.07 SE eggs/female and a loss of 0.86 ± 0.05 SE nestlings/female. Mean lifetime reproductive success for 350 females was 3.59 young ± 0.17 SE (range 0–18).

Rate of egg loss and nestling loss fairly uniform until last third of nestling phase, when there is little mortality (Holcomb 1972b). This is attributed to greater awareness of older nestlings, inconspicuous behavior in presence of predators, and older nestlings being less vulnerable to cool or wet weather.

Number Of Broods Normally Reared Per Season

Normally only 1 brood/season except in cases of predation or nest loss. Renesting after successfully fledging a brood is rare in northern populations (1 instance, n = 882 pairs, n = 1,168 nests; 1988–1997; se. Oregon; JAS), somewhat more common farther south (M. Whitfield pers. comm.).

LIFE SPAN AND SURVIVORSHIP

A few long-term studies. In s. Michigan, 9 of 22 males banded as adults were recaptured in subsequent years; 1 was at least 5 yr old at last capture, 2 were \geq 4 yr old, 2 \geq 3 yr old, and 4 \geq 2 yr old; 7 of 31 females returned and 6 were at least 2 yr old and 1 \geq 5 yr old at last capture (Walkinshaw 1966); in a followup of the previous study, 1 female banded in 1960 returned every year through 1966 and so was at least 7 yr old at last capture (Walkinshaw 1971). Longevity record of 7 yr from Bird Banding Lab records (Clapp et al. 1983).

Based on returns of 611 breeding Willow Flycatchers captured on Malheur NWR study areas in Oregon (1988–1997) that subsequently returned and bred, mean life span (not taking dispersal into account) of males was $1.08 \text{ yr} \pm 0.11 \text{ SE}$; females $0.97 \text{ yr} \pm 0.10 \text{ SE}$ (Sedgwick and Iko 1999). One individual, reported as having survived at least 8 yr following capture (Sedgwick and Klus 1997), was again recaptured (Aug 1998) and had survived at least 11 yr (JAS).

DISEASE AND BODY PARASITES

Diseases

No information.

Body Parasites

Parasitized by blow-fly larvae (Protocalliphora cuprina), as are Dusky and Western flycatchers (Boland et al. 1989). Alder Flycatcher is a known host of the louse-fly (Ornithomya bequaert; Whitman and Wilson 1992) and Ornithoctona fusciventris has been found in nests of Empidonax flycatchers (Hicks 1959). Northern fowl mites (Ornithonyssus sylviarum) were found in 1 Willow Flycatcher nest in se. Washington (King 1955) and in Wisconsin 60/141 nests were infested; maggots or pupae of the blow fly Protocalliphora sp. were found in 23 of 73 nests (McCabe 1991); no evidence of any effect of the mites or blow fly on flycatcher survival. Several instances of bill malformation reported (King 1955, Paxton et al. 1997, M. Whitfield pers. comm.).

CAUSES OF MORTALITY

Few data. Three major potential predators identified: in British Columbia, red squirrels suspected or observed predators of 45% of 60 nests. In se. Oregon, most nest predation believed to be mammalian, especially long-tailed weasel and mink (JAS). Predation the major cause of seasonal fecundity losses and is greater at egg stage than at nestling stage in Willow Flycatchers (Sedgwick and Iko 1999).

No information on effects of exposure or competition with other species.

RANGE

Initial Dispersal From Natal Site

Dispersal by juveniles variable: only 95 of 1,271 Willow Flycatchers (7.5%) produced in Oregon study areas and banded as nestlings or fledglings subsequently returned and bred (Sedgwick and Iko 1999); in s. California, however, 25.9% of birds banded as nestlings or fledglings (n = 286) returned to study area (M. Whitfield pers. comm.).

Fidelity To/Dispersal From Breeding Site And Winter Home Range

In s. California, 61.6% of adult males (n = 138)and 51.8% of adult females (n = 137) returned to the study area in a subsequent year (M. Whitfield pers. comm.). Over half of breeding adults captured in an Oregon study (1988–1997) returned to same general area and bred again in subsequent years (females: 186/347 [53.6%]; males: 138/264 [52.3%]; Sedgwick and Iko 1999); in subsequent years, median distance returning males (n = 362) and females (n = 349)moved from original nesting sites was 25 and 26 m, respectively (mean for males: 193 m ± 29 SE (range 0–4,662), females 233 m ± 37 SE (range 0–5,926; JAS). No information on fidelity to winter home range.

Home Range

One known estimate of wintering home range: roughly $1,100 \text{ m}^2$, somewhat smaller than territory size on breeding grounds (Gorski 1969a, 1969b).

POPULATION STATUS

Numbers

Very high densities possible: 218 individuals along 1.6 km of Buckeye Lake shoreline in Ohio (12 Jun 1928; Trautman 1940); 1 pair every 40 m along Blitzen River in se. Oregon (JAS); 3.1 nests/ha at study sites in Wisconsin, 1943-1977 (McCabe 1991). Typical density estimates from a range of habitats, regions: (a) 7.1, 7.1, and 10.6 territories/km², respectively, in 3 yr of study in an old-growth woods and swamp forest in Michigan (Knapp 1994, 1995, 1996); (b) 74, 86.4, and 111.1 territories/km², respectively, in 3 yr of study in a shrubby swamp and sedge hummock area in Connecticut (Magee 1994, 1995, 1996); (c) 24.7 and 24.7 territories/km², respectively, in 2 yr of study in a bulrush and cattail marsh in conifer forest in Montana (Bishop 1994, 1995); (d) 15 and 20 territories/km², respectively, in 2 yr of study in a mixed prairie in North Dakota (Johnson and Schwartz 1994, 1995); 34.6 pair/km²in Palouse Hills of se. Washington (King 1955); and (e) 27 and 27 territories/km², respectively, in 2 yr of study in old pasture shrub with hedgerows in Vermont (Merrill 1994, 1995).

Breeding Bird Surveys (Sauer et al. 1997) from 1966 to 1996 showed average of 1.17 Willow Flycatchers/route (n = 936 routes) in U.S. and 1.38 individuals/route for continent (n = 1,053 routes). Where sample size was adequate ($n = \ge 25$ routes), highest number of birds/route (7.30) was recorded in Southern Pacific Rain Forest.

Trends

BBS data (1966–1996) show a decreasing trend for both U.S. ($\leq 1.3\%$ /yr, p = 0.03) and continent ($\leq 1.2\%$ /yr, p = 0.01). Six states (Maine, Maryland, New Jersey, New York, North Dakota, and Pennsylvania) showed significant (p<0.05) population increases; Michigan, Oregon, and Washington showed significant population decreases (Sauer et al. 1997). *E. t. extimus* populations much reduced from historical levels, but no evidence of more recent declines since its listing as an Endangered species in 1995 (see Distribution: historical changes, above).

POPULATION REGULATION

Little information. Predation and brood parasitism are likely 2 greatest causes of reduction in seasonal fecundity (Sedgwick and Iko 1999; see Breeding: brood parasitism, above). Weather may occasionally regulate population growth through a reduction of food supply. In 1 year (1992) of a 10-yr Oregon study, 3-egg clutches were more common (58%; normally 4-egg clutches predominate), fecundity was lower (1.45 young/female) than in any of the other 9 yr, and numerous nestlings (about 9-12 d of age) perished from starvation. This coincided with low snowpack, below-normal spring precipitation, low riverflows, and dry marshes (JAS). During 12-yr study in Wisconsin, however, McCabe (1991) never observed food to be in short supply or limiting.

Conservation and Management

EFFECTS OF HUMAN ACTIVITY

Collisions With Stationary/Moving Structures Or Objects

Collisions of night migrants with towers are a source of mortality (Crawford 1976); effects on overall population unknown.

Degradation Of Habitat

Habitat destruction and degradation (Remsen 1978) and overgrazing by livestock (Serena 1982) major causes of decline. Types of damage by cattle include soil compaction and gullying (which dries meadows), grazing of willows, and changes in willow-foliage height and volume (Harris et al. 1987). Nests may also be directly destroyed by cattle as cows create and travel through "tunnels" in shrub willow riparian zones (Valentine et al. 1988). In Oregon, dramatic increases in Willow Flycatcher densities occurred following reduction in cattle-grazing and elimination of willow-cutting and spraying in Oregon (Taylor and Littlefield 1986); similarly, species was much more abundant in rarely grazed or undisturbed willow areas than in grazed willow areas in se. Oregon (Taylor 1986). In the West, association with riparian zones makes Willow Flycatchers vulnerable to variety of human influences (e.g., damming, dredging, channelization, urbanization, dewatering) that can impact flycatcher habitat. For example, formerly common along Colorado River upstream of Lees Ferry, an area now inundated by Glen Canyon Dam. Alteration of flooding cycles may affect nesting success; in some instances, Willow Flycatchers will not even attempt nesting in absence of flowing water (Johnson et al. 1999). Introduction and spread of tamarisk may be at least partly responsible for decline of Endangered E. t. extimus subspecies; an altered insect fauna (Carothers and Brown inadequate thermal 1991) or protection

compared to native broadleaf shrubs (Hunter et al. 1988) may be proximate factors. Many flycatcher populations (Arizona, New Mex-ico), however, use tamarisk and appear to have "average" nesting success, suggesting that tamarisk is mostly a symptom of dewatering and water regulation and does not adversely impact Willow Flycatchers per se (M. Whitfield pers. comm.).

Direct Human/Research Impacts

After Sedgwick and Klus 1997. Willow Flycatchers subject to injury caused by banding and color-banding. A leg-injury rate of 9.6% reported for birds returning to a study area in se. Oregon (59 of 617 returning birds had injured legs). Injuries ranged from minor (irritations on tarsus) to severe (amputation of foot) and return rates in year(s) following injury were lower (p =0.0003) for injured than uninjured birds. Injuries to adult females occurred at a higher rate than to adult males (p = 0.0003) and were more likely to occur on legs with 2 color bands (p = 0.001). Band injury apparently did not affect survival by reducing foraging efficiency as mass of injured and uninjured flycatchers did not differ (p >0.05). Similar band-injury rate (9.6–10.7%) reported for a s. California (E. t. extimus) population (n = 121-136 returns; M. Whitfield pers. comm.).

MANAGEMENT

Conservation Status

E. t. extimus subspecies recently listed as Endangered (U.S. Fish Wildl. Serv. 1995). Critical habitat for the subspecies was designated in 1997 in the 3 states (New Mexico, Arizona, and California) where largest populations are known to occur (U.S. Fish Wildl. Serv. 1997). Total number of E. t. extimus probably <1,000, with largest single population (243 pairs in 1999) along Gila River in sw. New Mexico (S. Stoleson and D. Finch pers. comm.). All other known populations consist of <40 pairs. All breeding E. t. extimus in California total <90 pairs (Small 1994); in Arizona, total population of extimus is only about 200 pairs. Population status of E. t. extimus even more critical as most populations (about 75%) are

small (<5 individuals) and widely separated from other breeding groups (U.S. Fish Wildl. Serv. 1997). Outside of habitat alteration and loss (see Effects of human activity, above) parasitism by Brown-headed Cowbirds may present largest conservation problem for *E. t. extimus*, as this subspecies is heavily parasitized in some areas; parasitism may be a major cause of decline in California and Arizona (Harris et al. 1987, Harris 1991, Brown 1994, Whitfield and Sogge 1999) and elsewhere.

Measures Proposed And Taken

Cowbird control (trapping, addling eggs, removing nestlings, and/or shooting) has been used as a management tool for several populations of Southwestern Willow Flycatcher, mostly in California (Rothstein 1994, Whitfield et al. 1999, Winter and McKelvey 1999).

Effectiveness Of Measures

In s. California, Willow Flycatcher nest success and young fledged/female increased from 23% and 1.04 young/female (n = 116 nests) before cowbird trapping (1989-1991; parasitism rate 63%) to 39% and 1.74 young/female (n = 178nests) after cowbird trapping (1993-1997; parasitism rate 22%). Little evidence of increase in number of flycatcher breeding pairs on study site, however, possibly due to a parasitism rate still considered too high for population to increase (Whitfield et al. 1999). Other factors (e.g., predation) thought to limit growth of this population, even with cowbird control. Another Willow Flycatcher population in s. California was stable during 6 yr of cowbird-trapping, and parasitism rates were low; uncertain whether flycatcher population stability could be attributed to cowbird-trapping, however, as there were no pretrapping data (Winter and McKelvey 1999). Cowbird-management programs may be needed to increase flycatcher reproductive success over short term, but ultimately, survival of E. t. extimus will depend on maintenance and restoration of riparian habitats.

Appearance

MOLTS AND PLUMAGES

Extent and sequence of molts not known for all subspecies; best known for E. t. traillii (= eastern) and E. t. brewsteri (= western) races; needs more study. Strategies appear to differ western between eastern and Willow Flycatchers. Eastern Willows (and Alder Flycatchers) replace flight feathers Jan-Mar, and both juveniles (second-years) and adults (aftersecond-years) replace most if not all flight feathers; apparently unknown whether feathers are replaced once between Aug and Apr (during a protracted Prebasic molt) or twice (a Prebasic and a Prealternate molt) in eastern populations (Pyle 1997a). Molt in western Willow Flycatchers proceeds as follows, below.

Hatchlings

Long, copious down (Mouse Gray) on crown, with tufts of shorter down (Pallid Neutral Gray) on spinal and alar tracts (King 1955, color names after Ridgway 1912).

Juvenal Plumage

Similar to Definitive Alternate plumage (see below) except wing-bars buffy brown-ish, upper parts duller and with brownish wash, and dark feather centers on crown-feathers (crown-spots) smaller (at least through Oct and probably through Feb; Pyle 1997a); breast olive-gray and sides more brownish (Oberholser 1974). Sexes alike. Fresher flight feathers also distinguish juveniles from adults during migration and at least through Oct. Skull ossification complete 15 Oct–Dec (possibly as early as 15 Sep in some California pop-ulations); some individuals retain windows through following spring (May; Pyle 1997a).

Basic I Plumage

Prebasic I (postjuvenal) molt is partial, including body plumage but few if any flight feathers or wing-coverts; occurs Sep–Nov (Dwight 1900, Dickey and van Rossem 1938, Pyle 1997a). Molt apparently begins during fall migra-tion, as some immatures showed evidence of body molt at Long Point, Ontario, en route south (Hussell 1991b); but see Hubbard 1987 and Unitt 1987, in which authors report that young flycatchers molt into Basic plumage prior to migration, which adds to the length of their stay on the breeding grounds. Plumage similar to Juvenal plumage (Pyle 1997a).

Alternate I Plumage

Prealternate I (Prenuptial) molt incompletecomplete and eccentric; occurs Mar-May (Pyle 1997a). A variable number of pri-maries (outermost 5-10) and secondaries (innermost 3-9) are molted; approximately 30% of western Willows, but 100% of eastern Willows (E. t. traillii and perhaps E. t. campestris) replace all remiges (Pyle 1998). Wing-feathers that are not replaced (innermost primaries and outermost secondaries) contrast with fresher, replaced remiges; fresh greater-coverts contrast with narrow, abraded primary-coverts (Pyle 1997a). Alternate I plumage alike for males and females. Similar to Definitive Alternate plumage (see below). Molt complete before spring migration begins, as there was essentially no molt in Willow Flycatchers captured at Long Point, Ontario, en route north (Hussell 1991a).

Definitive Basic Plumage

Definitive Prebasic (Postnuptial) molt was thought to occur on wintering grounds as early as 3 Sep; now known to begin during fall migration, as nearly all adults at Long Point, Ontario, showed some evidence of body molt, and a few individuals were replacing tailfeathers (Hussell 1991b). A complete molt, according to Dwight (1900) and Dickey and van Rossem (1938). Pyle (1997a) reports as incomplete-complete from Aug to Nov; some middle secondaries (S2-6) may be retained, and if so, are replaced during Definitive Prealternate molt. Primary-coverts broad, dusky, edged with brownish olive. Flight-feather replacement occurs Jan-Mar for E. t. traillii and Alder Flycatcher, either during a protracted Prebasic molt or during separate Prebasic and Prealternate molts (Pyle 1997a). Plumage similar to Definitive Alternate plumage.

Definitive Alternate Plumage

Partial-incom-plete molt, Mar-Apr, at least for *E. t. brewsteri* (Pyle 1997a); only secondaries 2–6 (at most) replaced if retained in Definitive Basic molt (above; Pyle 1997a). Outer primary-coverts broad, fresh, and dusky and do not contrast in wear with greater-coverts (compare with Alternate I plumage).

Plumage description after Ridgway 1907: Plain olive above; crown and hindneck slightly grayer; rump and upper tail-coverts paler and more brownish olive; tail deep gravish brown, outer webs of inner rectrices olive and outermost ap-proaching dull whitish; wings darker gravish brown, median and greater wingcoverts tipped with pale olive or pale buffy gravish brown, forming 2 wing-bars (posterior wing-bar paler); secondaries edged on outer web with whitish, tertials similarly but more broadly edged; eye-ring and lores olive-whitish, lores intermixed with dusky; sides of head and neck slightly paler and grayer than upperparts; chin and throat white; breast and sides pale brownish gray or olive-gray and flanks pale olive or greenish olive; rest of underparts white tinged with pale primrose yellow on flanks and under tail-coverts; axillars and under wing-coverts pale prim-rose yellow; inner webs of remiges edged with pale gravish buff.

BARE PARTS

Bill And Gape

Upper mandible dusky brown to brownish black; lower mandible pale brownish or brownish white (Ridgway 1907) or entirely or mostly yellowish or pinkish (Pyle 1997a). Inner mouth lining bright orangish (Phillips et al. 1966) or orange-yellow (Pyle 1997a).

Iris

Brown (Ridgway 1907).

Legs And Feet

Dusky brown to brownish black (Ridgway 1907); blackish (Phillips et al. 1966, Pyle 1997a).

Measurements

LINEAR

After Walkinshaw 1966 . Wing (means, mm): male, 70.9 (range 65–75, n = 28); female, 66.6 (range 65–72, n = 38). Tail: male, 58.4 (range 53–60.5, n = 28); female, 55.2 (range 52–61, n =38; s. Michigan birds). For additional measurements, see Ridgway 1907, Pyle 1997a, and Table 1; for comparisons among subspecies, see Unitt 1987.

Bill measurements useful in combination with wing and tail measurements to differentiate sexes (males generally with longer wings and tails, and longer, narrower bills). Differences among sub-species slight; wing formula in combination with plumage color useful for differentiating 2 eastern from 3 western subspecies (Unitt 1987).

Specimen shrinkage a general phenomenon and occurs in both Willow and Alder flycatchers; may affect sexing guidelines applied to monochromatic living birds when developed from museum spec-imens unless correction factors applied; tail shrink-age for Alder and Willow Flycatchers combined, for example, is 2.8% (Winker 1993).

Mass

In New Mexico, mean mass 12.7 g \pm 1.2 SD (range 10.3–15.9, n = 84 migrants; sex[es] unknown; Yong and Finch 1997). In Michigan, average mass of breeding males, 12.9 g (range = 11.4–14.7, n = 18); breeding females, 12.3 g (range 10.2–14.2, n = 22; Walkinshaw 1966). Mean mass of breeding season adults from se. Oregon: males 12.72 g \pm 0.70 SD (n = 373); females 12.47 g \pm 1.12 SD (n = 369; Sedgwick and Klus 1997).

	Males	Females
Bill length ¹	9.12 ± 0.070	8.85 ± 0.047
_	(8.0–10.3, 47)	(8.4–9.5, 19)
Wing-chord	70.55 ± 0.238	67.01 ± 0.120
length ²	(67.5–74.5, 50)	(64.4–70.2, 18)
Tail length	59.01 ± 0.264	57.27 ± 0.413
-	(56.3–63.9, 49)	(54.0–59.9, 18)
Tarsus length	16.47 ± 0.090	16.67 ± 0.113
	(15.1–17.5, 50)	(15.8–17.5, 18)
Hind-toe	11.40 ± 0.079	11.11 ± 0.125
length ³	(9.6–12.4, 49)	(10.0–12.0, 19)
¹ Anterior margin of nostril to bill tip.		
² Wing-chord.		
³ Hind toe with claw = distance between the proximal		

³ Hind toe with claw = distance between the proximal end of the hallux and the distal end of its claw.

Table 1. Average measurements of WillowFlycatchers.

Priorities for Future Research

Because of its confusing taxonomic history and the recent endangerment of the southwestern subspecies, the Willow Flycatcher is relatively well known. Much of the recent research on this species has occurred in the southwestern United States on the endangered E. t. extimus. Topics of current, planned, and needed research to improve management and effect recovery of the subspecies include: (1) studies of the geographical corres-pondence of morphological, genetic, and vocal differentiation to better define the geographical range of E. t. extimus; (2) improved knowledge of historic and current distribution and habitats to understand causes and patterns of decline; (3) more detailed understanding of direct human impacts such as water development, grazing, recreation, and pesticide use; (4) studies of the effects of exotic vegetation on flycatcher reproductive success and prey abundance; evaluation of the need for and potential effects of tamarisk biocontrol; (5) because many populations of E. t. extimus are small, studies of the effects of small population size and reduced genetic variation on population

viability are needed; (6) determination of how serious a threat cowbird parasitism is, how it varies with landscape, habitat, and distribution of cattle, and whether trapping should be widely used as a temporary strategy to effect recovery; (7) winter population studies to identify habitat selection and preferences, factors limiting winter survival, and inter- and intraspecific resource competition; (8) migration studies to identify important migration stopovers, determine habitat use, and evaluate migrant condition and stopover time; and (9) studies of demography and population dynamics to identify source and sink populations, survivorship, fidelity, age structure, and recruitment.

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