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Chapter 6: Breeding Season Ecology

The willow flycatcher (*Empidonax traillii*) breeds across much of the conterminous United States and in portions of extreme southern Canada. As might be expected in such a wide-ranging species, willow flycatchers in different portions of the range exhibit differences in appearance, song, and ecological characteristics. The intent of this chapter is to provide information on the breeding-season ecology of the southwestern subspecies, *E.t. extimus*. However, most ecological studies to date have dealt with other willow flycatcher subspecies. Relatively few studies have been published on *E.t. extimus*, and much of what is currently known is presented in unpublished literature (e.g., agency and consulting firm reports); these sources are relied upon heavily in this chapter. This chapter does not address habitat characteristics in depth, other than for nest sites (refer to *A Survey of Current Breeding Habitats* for additional details). Although southwestern willow flycatchers are frequent victims of nest parasitism by brown-headed cowbirds (*Molothrus ater*), this chapter will not address the topic of parasitism and its effect on breeding ecology (refer to *The Ecology of Brown-headed Cowbirds and their Effects on Southwestern Willow Flycatchers* for details). Readers interested in more details of willow flycatcher biology and ecology are encouraged to read McCabe's (1991) treatise, which is based on over a decade of willow flycatchers research in Wisconsin and includes comparisons with other populations and subspecies.

Breeding Range and Taxonomy

The willow flycatcher is one of 11 *Empidonax* flycatchers that breed in North America. Although the *Empidonax* flycatchers are considered a very difficult group to identify by sight alone, each has unique morphological features, vocalizations, habitats, behaviors, and/or other traits that have allowed taxonomists and biologists to characterize each species. The willow flycatcher differs from most other *Empidonax* in lacking a conspicuous eye-ring, and having both a completely yellow lower mandible and a whitish throat that contrasts with a pale olive breast. While these differences may be subtle, the willow flycatcher also has a distinctive song (often termed *fitz-bew*; see below) that clearly separates it from all other bird species.

The willow flycatcher was first described by J.J. Audubon, who collected a specimen in the woods along the Arkansas River in the early 1800s (Audubon 1831) and named it *Muscicapa traillii*. Since that time, the species has undergone a series of name changes and species/subspecies designations (see Aldrich 1951, Browning 1993). Prior to 1973, the willow flycatcher and alder flycatcher (*Empidonax alnorum*) were

treated together as the Traill's Flycatcher (A.O.U. 1957), but subsequent work proved that they do not interbreed (Stein 1958, 1963), have different vocalizations (Stein 1958), and are genetically distinct (Seutin and Simon 1988). The American Ornithologist's Union (1973) accepted the separation of willow and alder flycatchers in 1973. McCabe (1991) reviews the many common names historically given to the willow flycatcher.

The southwestern subspecies was first described by Phillips (1948). Unitt (1987) re-evaluated the subspecies taxonomy of the willow flycatcher and recognized four subspecies, each with a distinct breeding range and differentiated primarily by subtle differences in color and morphology. Browning (1993) performed a similar evaluation and proposed five subspecies, rather than four. Both authors, however, reconfirmed the validity of *E.t. extimus*, which has also been accepted by most authors (Aldrich 1951, Behle and Higgins 1959, Phillips et al. 1964, Oberholser 1974, Monson and Phillips 1981, Schlorff 1990, USFWS 1993). Based on Unitt (1987) and Browning (1993), the breeding range of the southwestern willow flycatcher (Figure 6-1) includes southern California (from the Santa Ynez River south), Arizona, New Mexico, southwestern Colorado, extreme southern portions of Nevada and Utah, and western Texas (although recent breeding records from west Texas are lacking). Records of probable breeding southwestern willow flycatchers in Mexico are few and restricted to extreme northern Baja California del Norte and Sonora (Unitt 1987, Wilbur 1987).

The southwestern willow flycatcher is generally paler than other willow flycatcher subspecies (Unitt 1987), although this difference is indistinguishable without considerable experience and training, and without study skins as comparative reference material. All three western subspecies differ from E.t. traillii in wing formula (Unitt 1987). Differentiation of subspecies in the field is not reliable, due to the subtlety of morphological differences, inconsistent conditions for comparisons, and the inability to repeat or reassess the identifications of individual specimens (Hubbard 1999).

Vocalizations

Willow flycatchers are suboscines, and their songs appear to be innate, rather than learned (Kroodsma 1984). In fact, even hatching-year flycatchers can sing (Kroodsma 1984, Sogge 1997). As with most birds, singing behavior is regulated by hormone levels, which in turn are influenced by a number of factors including photoperiod, time of day, and auditory and visual stimuli from other birds of the same species (Kroodsma 1984, Catchpole and Slater 1995).

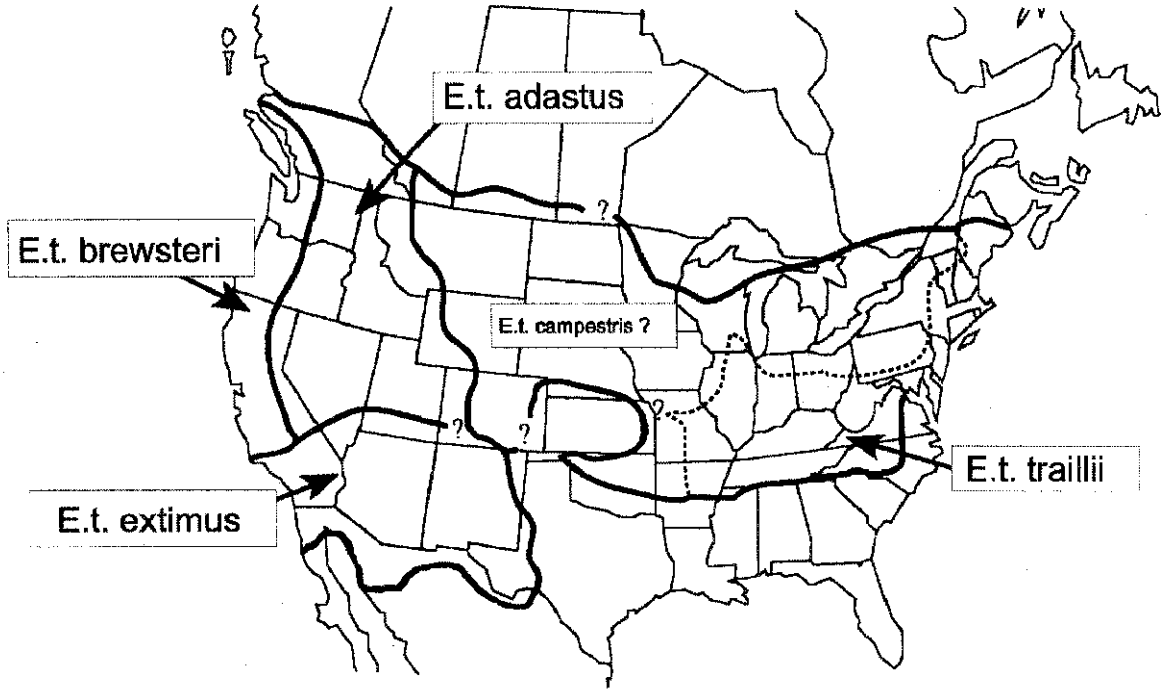

Figure 6-1. Breeding range distribution of the subspecies of the willow flycatcher (*Empidonax traillii*). Adapted from Unitt (1987), Browning (1993) and Sogge et al. (1997a).

The willow flycatcher has a distinct primary song, often referred to as *fitz-bew*, that distinguishes it from all other *Empidonax* flycatchers, and from other birds in general (refer to Stein 1963 for a detailed discussion). This is the primary territory advertising song of male willow flycatchers, and all subspecies sing *fitz-bew*. Singing bouts are usually comprised of a series of *fitz-bews*, sometimes interspersed with *creet* notes, lasting from less than a minute to over a half-hour.

Breeding males sing to advertise their territory to prospective mates and other nearby males. Males sing from a series of song perches throughout their territory, usually from tall perches but sometimes from within dense vegetation. Weydemeyer (1973) and McCabe (1991) described willow flycatchers singing during flight in the evenings, but this has been observed only rarely in *E.t. extimus*. Migrant willow flycatchers often sing from tall song perches during spring migration, in much the way that territorial birds do (Johnson and Sogge 1997). Sogge et al. (1997b) found that migrants accounted for up to 64% of the spontaneously singing flycatchers found each year along the Colorado River in the Grand Canyon. This makes it difficult if not impossible to separate territorial birds from migrants based on singing behavior alone.

Female willow flycatchers also sing, at least in some circumstances. Seutin (1987) reported female willow flycatchers singing in response to tape-playback experiments in southern Canada. Although he clearly established that females sing, the extent of female song under non-experimental conditions was unknown. Until recently, it was generally assumed that females seldom sang, and/or that their songs were quieter and/or not given from song perches in the way that males sing (Sedgwick and Knopf 1992). New research, much of it with banded individuals of known sex, has shown that female southwestern willow flycatchers regularly sing (though not nearly as often as males). Female flycatchers sometimes sing more quietly than males and sometimes near the nest (Sogge et al. 1997b, M. Whitfield unpublished data), but will also sing loudly and persistently from song perches, as is characteristic of males (Paxton et al. 1997). The true extent and function of female song awaits further research, but it is clearly incorrect to assume that all loudly singing willow flycatchers are males.

Male willow flycatchers sing most persistently early in the breeding season, but song rate declines as the season progresses, particularly once the male finds a mate and nesting efforts begin. Territorial flycatchers often begin singing well before dawn (as early as 0330 hrs standard time), and song rate is generally highest early in the morning. Short periods of predawn singing often continue as late as July (Sogge et al. 1997b). In breeding groups with many territorial males, song rate may remain high throughout most of the breeding season. Males may sing up to 60 songs per minute (H. Yard and B. Brown unpublished data). Unmated males and males with territories near other willow flycatchers tend to vocalize more than males in isolated territories (M. Sogge and M. Whitfield, unpublished data).

Being highly territorial, willow flycatchers readily sing and/or call in response to broadcast tapes of willow flycatcher song (Gorski 1969, Tibbitts et al. 1994), which they apparently perceive as an intruding flycatcher. This ready response to taped vocalizations forms the basis of standardized survey protocols currently in use (Craig et al. 1992, Sogge et al. 1997a). In many cases, willow flycatchers that are not vocalizing when surveyors first arrive at a site begin singing in response to a broadcast taped song. Territorial breeding males and females, migrants, and (perhaps rarely) even recently fledged (6-8 week old) willow flycatchers will respond to tape playback (Sogge 1997, Sogge et al. 1997a). However, much as with the general song patterns, response to tape playback declines over the course of the breeding season, and breeding flycatchers may not respond strongly after nesting has begun.

Another common vocalization used by flycatchers is the *whitt* call, which is frequently given by both sexes. *Whitts* are given as an alarm call and during interactions between flycatchers. *Whitt*s are often the most common vocalization used during mid- and late breeding season. Many other bird species have similar *whitt* calls, so unlike the *fitz-bew*, the *whitt* is not generally considered unique to willow flycatchers.

Foraging and Food

Foraging Behavior

The willow flycatcher, as the name implies, is primarily an insectivore. It is an agile aerialist, capable of catching flying insects on the wing. It often does so by darting quickly out on short flights, catching an insect in its bill, then returning to the same or a nearby perch. Another common foraging behavior is gleaning, where they hover to pick insects off of leaves and other vegetation. Willow flycatchers will also drop to the ground to capture insects, and females sitting on nests will sometimes reach out and pluck insects that are crawling nearby. Larger prey (such as dragonflies or butterflies) is often beaten against the perch, killing and softening it prior to consumption. Flycatchers forage within and above the canopy, along the patch edge, in openings within their territory, and above surface water.

Prescott and Middleton (1988) reported that willow flycatchers in Ontario spent 5 percent of time foraging and 63 percent sitting, corresponding to a “sit and

wait" foraging tactic whereby birds can simultaneously engage in vigilance, food searching and capture, territorial advertisement, and resting. Preliminary studies on southwestern willow flycatchers documented foraging rates 0 to 4.6 foraging events per minute, with foraging rate highest early and late in the day, and during the nestling period (H. Yard and B. Brown, unpublished data).

Prey Items

All North American *Empidonax* flycatchers appear to have generally similar diets during the breeding season (e.g., predominantly small to mid-sized insects; Beal 1912). Most available information on specific prey items of willow flycatchers comes from studies of subspecies other than *E.t. extimus*, which demonstrate that the species is somewhat of a generalist. Overall, wasps and bees (Hymenoptera) are the most common food items, with beetles (Coleoptera), flies (Diptera), and butterflies/moths and caterpillars (Lepidoptera) being other major components (Beal 1912). Vegetable foods such as berries and small fruits have been reported (Beal 1912, Roberts 1932, Imhof 1962), but overall do not appear to be a significant food source during the breeding season (McCabe 1991).

A study of diet of adult southwestern willow flycatchers (Drost et al. 1997) found a wide range of prey taken. Major prey items were small (flying ants) to large (dragonflies) flying insects, with Hymenoptera, Diptera, and Hemiptera comprising half of the prey items. Willow flycatchers also took non-flying species, particularly Lepidoptera larvae. Plant material was negligible, consisting of a few seeds in several samples.

McCabe (1991) studied the insects brought by adults to nesting willow flycatchers (*E.t. traillii*) in Wisconsin. He found 33 families of invertebrates in a total of 214 food items sampled from eight nests. The most prevalent items were flies (Diptera), butterflies (Lepidoptera), spittlebugs (Homoptera), and beetles (Coleoptera). Immature and non-flying adult insects comprised 30 percent of the total; spiders accounted for 26 percent of the non-flying food items. This suggests that nestlings are fed similar, if perhaps somewhat smaller, food items to those consumed by adults.

Breeding Chronology

A neotropical migrant, southwestern willow flycatchers generally spend only three to four months on their breeding grounds. The remainder of the year is spent on migration or in wintering areas south of the United States (see the Migration and Wintering section). During the relatively short time they are on their breeding grounds, willow flycatchers must find a territory and a mate, build the nest, lay and incubate eggs, raise their young, and care for the fledged young. Figure 6-2 presents a generalized breeding chronology for the southwestern willow flycatcher (based on Unitt 1987, Brown 1988, Whitfield 1990,

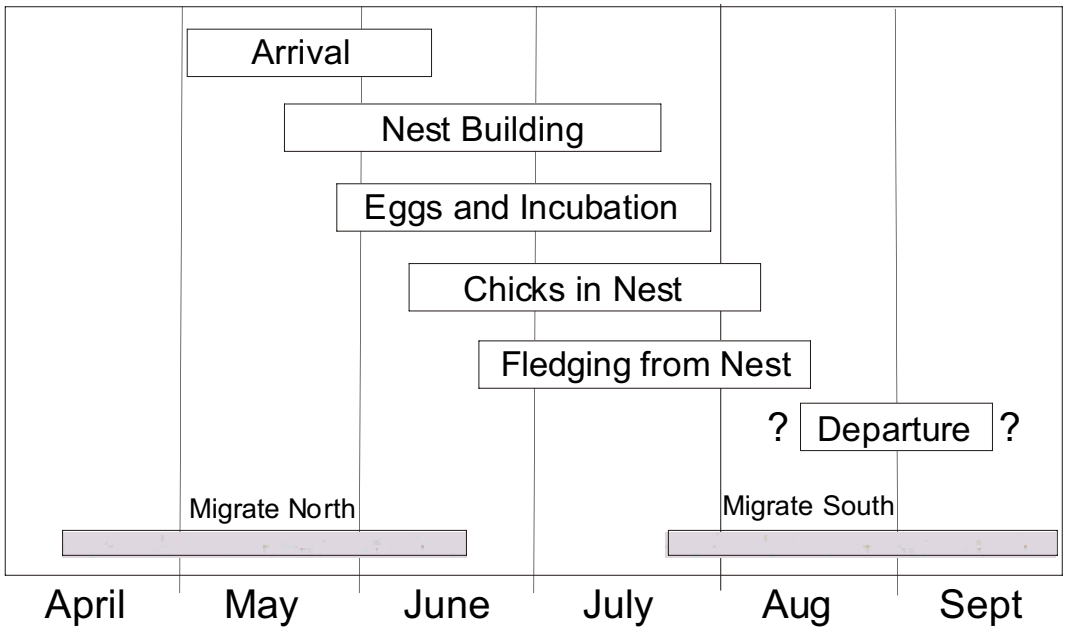

Figure 6-2. Generalized breeding chronology of the southwestern willow flycatcher (from Sogge et al. 1997a). Dates for a given stage may vary a week or more at a given site or during a given year.

Skaggs 1996, Sogge 1995, Maynard 1995, Sferra et al. 1997, and Sogge et al. 1997b). Record or extreme dates for any stage of the breeding cycle may vary as much as a week from the dates presented. In addition, flycatchers breeding at higher elevation sites, and other subspecies in more northerly areas, usually begin breeding efforts several weeks later than those in lower, southern areas.

Southwestern willow flycatchers typically arrive on breeding grounds between early May and early June, although a few individuals may establish territories in very late April (Unitt 1987, Maynard 1995, Skaggs 1996, Sferra et al. 1997). Because arrival dates vary geographically and annually, northbound migrant willow flycatchers (of all subspecies) pass through areas where *E.t. extimus* have already begun nesting. Similarly, southbound migrants (again, of all subspecies) in late July and August may occur where southwestern willow flycatchers are still breeding (Unitt 1987). Therefore, it is only during a short period of the breeding season (approximately 15 June through 20 July) that one can assume that a willow flycatcher seen within *E.t. extimus* range is most likely of that subspecies.

Nest building usually begins within a week of pair formation. Egg laying begins (rarely) as early as late May, but more often starts in early to mid-June. Chicks can be present in nests from mid-June through early August. Young typically fledge from nests from late June through mid-August; later fledglings are often products of renesting attempts. Adults depart from breeding territories as early as mid-August, but may stay until mid-September if they fledged young late in the season (M. Whitfield and W. Haas, unpublished data). Almost nothing is known regarding movements and ecology of adults and juveniles after they leave their breeding sites. Males that fail to attract or retain mates, and males or pairs that are subject to significant disturbance (such as repeated nest parasitism, predation, etc.) may leave territories by mid-July (Sogge 1995, Sogge et al. 1997b). Fledglings probably leave the breeding areas a week or two after adults; in Southern Ontario southward migration dates of immatures occurred 15 days later than for adults (Hussell 1991).

Mating and Territoriality

The southwestern willow flycatcher breeds only in dense riparian habitats, from sea level in California to over 2600 m in Arizona and southwestern Colorado (Sogge et al. 1997a). Although other willow flycatcher subspecies may breed in shrubby habitats away from water, *E.t. extimus* breeds only in dense riparian vegetation near surface water or saturated soil. Other characteristics such as dominant plant species, size and shape of habitat patch, canopy structure, vegetation height, etc., vary widely among sites (refer to *A Survey of Current Breeding Habitats*).

The first flycatchers to arrive at a breeding site are generally males, which establish a territory by singing and aggressive interactions with other flycatchers. Willow flycatchers are very territorial, and will sing almost constantly throughout the day when establishing their territory. Females tend to arrive later (approximately a week or two) and settle on the territory of a male. It is not known exactly what factors a female uses to select a territory, though it may be related to some factor of habitat quality or potential quality of the male. Second year males arrive at about the same time as females (M. Whitfield, unpublished data).

Males are usually monogamous, but annual polygyny rates of approximately 10-15% have been recorded at the Kern River Preserve in California (Whitfield and Enos 1996, 1998). Polygyny has also been recorded in Arizona (Sferra et al. 1997, Sogge et al. 1997b, Langridge and Sogge 1997, Paradzick et al. 1999). Polygynous males typically have only two females in their territory, but there have been several cases of a male with three and four females in a single year (Whitfield and Sogge, unpublished data). Preliminary genetic evidence also suggests that extra-pair copulation occurs, wherein one or more nestlings in a nest are fathered by a flycatcher other than the territorial male for that nest (Paxton et al. 1997).

Initial data from studies of color-banded populations in Arizona (Paxton et al. 1997, Netter et al. 1998) suggest that between-year mate fidelity may be low, and that during a breeding season some flycatcher pairs break up and subsequently pair and breed with other individuals. Whitfield (1980, unpublished data) also documented two cases where pairs that were together early in the season broke up and mated with other flycatchers later that same season. Such pair "reshuffling" may be related to initial nest failure, but additional data are needed to test this.

Southwestern willow flycatcher are strongly territorial, and will defend their breeding area from other flycatchers. Flycatcher territories (defined as a defended area, per Noble 1939) are often clumped together, rather than spread evenly throughout a habitat patch. This has led some authors to label willow flycatchers as "semi-colonial" (McCabe 1991), although they do not fit the true definition of a colonial species and regularly breed at sites with only one or a few pairs (Sferra et al. 1997, Sogge et al. 1997a and 1997b). The Least Flycatcher (*Empidonax minimus*) also tends to breed in groups (Briskie 1994).

Territory size varies greatly, probably due to differences in population density, habitat quality, and

nesting stage. Early in the season, territorial flycatchers may move several hundred meters between singing locations, although this has been documented only at sites with one or two territorial males (Sogge et al. 1995, Petterson and Sogge 1996, R. Marshall pers. comm.). During incubation and nestling phases territory size, or at least the activity centers of pairs, can contract and be very small. Mapped breeding territory sizes are 0.06 to 0.2 ha for flycatchers occupying 0.6-0.9 ha patches on the Colorado River, AZ (Sogge et al. 1997b), 0.2 to 0.5 ha in a 1.5 ha patch along the Verde River, AZ (Sogge 1995), and 0.14-2.3 ha along the Kern River, CA (Whitfield and Enos 1996). Estimated territory sizes at the Gila River near Cliff, NM ranged from approximately 0.2 to >1 ha per territory (Skaggs 1996). Reported territory sizes of other willow flycatcher subspecies are also variable; 0.09 ha (Trautman 1940), 0.3 ha (McCabe 1991), 0.4 ha (Walkinshaw 1966), and 1 ha (Gorski 1969). However, only Gorski's (1969) study was based on detailed observations of color-banded individuals, and territory sizes for other studies must be viewed as approximations.

Territories of polygynous males are often larger than those of monogamous males (M. Whitfield pers. comm.). Flycatchers may use a larger area than their initial territory after their young are fledged, and utilize non-riparian habitats adjacent to the breeding area. Even during the nesting stage, adult flycatchers sometimes fly outside of their territory (often through the "air space" of an adjacent territorial flycatcher) to forage for their nestlings.

Site Fidelity

It is often assumed that most passerine birds, particularly those that are highly territorial, exhibit strong breeding site fidelity between and within years. Until recently, this was thought to be the case with the southwestern willow flycatcher. Repeated annual survey efforts on unbanded willow flycatcher populations (Sogge 1995, Sferra et al. 1997, Sogge et al. 1997b) found that the location and boundaries of individual flycatcher territories were often very similar in successive years, leading to speculation that the same male was holding the territory each year and that site fidelity was therefore high.

Evidence gathered during multi-year studies of color-banded populations (Figure 6-3) shows that although most male flycatchers return to former breeding areas, southwestern willow flycatchers regularly move among sites within and between years. Between 1996 and 1997, 29 percent of banded willow flycatchers in Arizona returned to the breeding site of the previous year, while 11 percent moved to other breeding areas within the same major drainage (Paxton et al. 1997). The remaining 60 percent of flycatchers were not relocated in 1997, and may have died or moved to undiscovered breeding sites. Distance moved ranged from 2 to 30 km, and movements were not always to the next closest breeding area. Among those flycatchers returning to the same breeding site between years, 23 percent moved to a different part of the habitat patch. Distance moved ranged from 20 to 900 m. There were also two cases of movement (>500 m) within a breeding site during the course of a breeding season. Thus, although most returning flycatchers showed site fidelity to breeding territories, a significant number move within and among sites. The mechanisms controlling the decision to return or move, as well the adaptive value of movement between sites, are unknown. Such movement does increase gene flow among breeding groups, which provides for higher genetic diversity than if movements did not occur.

In some cases, willow flycatchers are faced with a situation that forces movement, such as when catastrophic habitat loss occurs. In 1996 and 1997, occupied flycatcher breeding habitat was destroyed by fire at two sites, one along the San Pedro River in Arizona (Paxton et al. 1996) and the other along the Gunnison River in southwestern Colorado (Owen and Sogge 1997). In Arizona, the willow-cottonwood habitat was completely burned during the breeding season as nesting was underway, destroying all or most of seven territories. At least four nests were lost, and all willow flycatchers abandoned the site within a week after the fire and were not seen again that year. No willow flycatchers attempted to breed in the burned area in 1997. Seven displaced flycatchers were resighted in 1997; two had moved to unburned areas within the breeding site, and five moved to other breeding areas

Figure 6-3. A color-banded southwestern willow flycatcher. Photo by Michael Moore.

between 2 and 28 km away. In Colorado, virtually all of the tamarisk (*Tamarix ramosissima*) and willow habitat was destroyed, leaving only charred sticks and a few small scattered live willows. Surprisingly, some flycatchers returned to the burned areas and attempted to breed, even in areas without any live vegetation. However, pairing success and subsequent productivity was negatively affected. Several southwestern willow flycatcher breeding populations also face potential habitat loss due to flooding from rising reservoir levels. Where and how far these displaced flycatchers will move is uncertain and the subject of on-going studies (e.g., Paxton et al. 1997).

Nests and Eggs

Southwestern willow flycatchers build open cup nests constructed of leaves, grass, fibers, feathers, and animal hair; courser material is used in the nest base and body, and finer materials in the nest cup (Figure 6-4). Willow flycatcher nests sometimes have 2-15 cm of loose material dangling from the bottom of the nest. In tamarisk-dominated habitats, nests may be constructed completely of tamarisk leaves and have no hanging material from the bottom (Figure 6-5). Nests are approximately 8 cm high and 8 cm wide (outside dimensions), exclusive of any dangling material at the bottom.

Figure 6-4. Willow flycatcher nest placed in a willow near Alpine, AZ. Photo by Mark Sogge.

Females build the nest, with little or no assistance from the male, over a period of four to seven days (although renests are often built in as little as two or three days). McCabe (1991) conducted detailed studies of nest building *E. t. traillii* and found that females brought and added material to the nest every 7 to 10 minutes. Most nests are used only once, although females will often use some fibers and materials (particularly the lining) from the original nest when constructing a subsequent nest during the same season (McCabe 1991). There are only a few recorded instances of reuse of the same nest during a breeding season (H. Yard, B. Brown, and Arizona Game and Fish Department unpublished data) and no records of reuse between years.

Typical nest placement is in the fork of a branch with the nest cup supported by several small-diameter vertical stems. The main branch may be oriented vertically, at an angle, or (rarely) horizontally and stem diameter for the main supporting branch can be as small as 2 to 4 cm. Vertical stems supporting the nest cup are typically 1 to 2 cm in diameter. The nest materials are interwoven among the supporting branches and twigs, such that nests cannot readily be separated from the branches without destroying the nest. McCabe (1991) studied details of *E. t. traillii* nest placement, and found that a network of main and support branching stems are the key to nest placement. Main nest support stem diameter averaged 1.3 cm, and support branches averaged between 2 and 5 cm diameter. Each nest included an average of five support branches, most of which angled upward between 40 and 70 degrees (with a peak at 50 to 60 degrees). Such supporting branch systems are typical of southwestern willow flycatcher nests as well.

Nest height varies considerably (from 0.5 to 18 m), and may be correlated with height of nest plant, overall canopy height, and/or the height of the vegetation strata that contains small twigs and live growth. In Arizona and California, flycatchers using mainly native broadleaf riparian habitats often nest relatively low (usually 2 to 3 m above ground; Sferra et al. 1997, Whitfield and Enos 1996), whereas those using mixed native/exotic and monotypic exotic riparian habitats often nest higher (usually 4 to 7 m above ground; Sferra et al. 1997, Sogge et al. 1997b). However, in any habitat type, nests may be found wherever the appropriate twig structure and plant cover occurs, at almost any height and location (near the center or

Figure 6-5. Southwestern willow flycatcher nest placed in tamarisk at Roosevelt Lake, AZ. Photo by Renee Netter.

on the edge of the nest bush). For example, flycatchers sometimes nest >10 m high in native-dominated habitats along the San Luis Rey River, CA (W. Haas, unpublished data) and the Gila River, NM (Stoleson and Finch 1999). At such sites nest height is linked to the tree species that dominates the site.

Prior to 1950 the vast majority of southwestern willow flycatcher nests were found in willows (Grinnell and Miller 1944, Phillips 1948, Phillips et al. 1964, Hubbard 1987, Unitt 1987). This is not surprising, given that willows were prevalent in streamside riparian stands in the southwest and that young willows can provide the dense cover and fine branching structure favored by nesting flycatchers. However, as the southwest experienced reduction and loss of native riparian vegetation and the invasion of several exotic plants, the willow flycatcher adapted to new host plants and now nests in both native and introduced species.

At high elevation sites in Arizona and southwestern Colorado, Geyer (*Salix geyeriana*) and other willows are used almost exclusively for nesting (Owen and Sogge 1997, Sferra et al. 1997). Along the Gila River in Grant County, New Mexico, 76 percent of southwestern willow flycatcher nests were placed in boxelder (*Acer negundo*), the dominant understory species, with the remainder in other native and exotic plants (Skaggs 1996). Saltcedar is the most frequent nest substrate in Arizona (Brown 1988, Paradzick et al. 1999) and New Mexico (Hundertmark 1978, Hubbard 1987, S. Williams pers. comm.), and is also used for nesting in Colorado, Nevada, and Utah (Owen and Sogge 1997, Langridge and Sogge 1998, McKernan and Braden 1999; M. Sogge unpublished data). Nests are often placed in tamarisk even when native vegetation is present and/or predominant in a territory (Sferra et al. 1997, Owen and Sogge 1997, Paradzick et al. 1999, USFWS unpublished data). However, not all tamarisk habitat appears suitable for nesting flycatchers. Willow flycatchers nest in Russian olive (*Elaeagnus angustifolia*) at some New Mexico breeding sites (Hubbard 1987, Maynard 1995, Cooper 1996 and 1997). In California, most nests are in native vegetation including willow and stinging nettle (*Urtica* spp.; Holmgren and Collins 1995, Whitfield and Enos 1996). In a very unusual situation along the San Luis Rey River in San Diego County, California, approximately 90 percent of flycatcher nests were in live oak (*Quercus agrifolia*), which became the dominant plant species adjacent to the river following willow removal in the 1950s (W. Haas, pers. comm.). McCabe (1991) demonstrated somewhat similar switching between nest substrates in Wisconsin as substrate availability changed among years. Southwestern willow flycatcher nests have also been found in buttonbush, black twinberry (*Lonicera involucrata*), Fremont cottonwood, alder (*Alnus* spp.), blackberry (*Rubus ursinus*), baccharis (*Baccharis* spp.) and other plants. Overall, the plant species appears less important than the appropriate live foliage density and twig structure.

Willow flycatcher eggs are buffy or light tan, generally with brown markings in a wreath at the blunt end but occasionally unspotted (Bent 1942). Eggs are approximately 18 mm long and 14 mm wide, and weigh about 1.6 g (McCabe 1991). Clutch size is usually 3 or 4 eggs for first nests, and is typically smaller in Arizona and New Mexico (usually 3) than in California and elsewhere in the species' range (usually 4; McCabe 1991, M. Whitfield unpublished data). The reasons for these differences are not known, but may be related to food availability or condition of the breeding female (Lack 1954). Female flycatchers lay one egg per day, although some four egg clutches may take five days to lay.

Females generally do not begin incubating until the entire clutch has been laid. Incubation generally lasts 12-15 days from the date the last egg is laid. McCabe (1991) gave a mean incubation period for *E.t. traillii* of 14.84 days (n=50 nests), and found that in 97 and 82 percent of three and four egg clutches, respectively, all eggs in a nest hatch within 48 hrs of each other. He also recorded a 3 percent rate of infertile or addled eggs. After hatching, females carry the eggshell fragments away from the nest.

Most incubation is by the female, although males have been recorded incubating in Arizona (H. Yard, B. Brown, and Arizona Game and Fish Department unpublished data). Incubating females sit tightly in the nest cup, with head and tail protruding over the nest edge. Females spend approximately 50 percent of the day attending (incubating or shading) the eggs (H. Yard and B. Brown unpublished data), and incubate throughout the night (Arizona Game and Fish Department unpublished data). Daytime incubation and shading bouts last from less than one to more than 60 minutes. Shading females stand on the nest rim or within the nest cup, positioned to provide shade to the eggs when the nest received direct sunlight. When shading during the heat of the day, females often appear heat-stressed, panting with mouth open.

Nestlings and Parental Care

Nestlings hatch out (on day 0) weighing only 2 g, mostly naked with only sparse gray down and the yolk sac still visible. Young hatch with the help of an egg tooth, which is no longer visible after the first week (King 1955, McCabe 1991). The edge of the bill and inside of the mouth of nestlings are bright yellow (Figure 6-6), as opposed to the orange mouth linings of brown-headed cowbirds (Tibbitts et al. 1994). Recently hatched flycatchers are unable to lift their head or move about, and motor coordination does not develop until days 2 or 3. Nestlings grow rapidly, reaching about 14 g by day 10. Feather development also occurs quickly, with most body and flight feathers

Figure 6-6. Nestling southwestern willow flycatcher. Note the yellow edge of bill and mouth lining. Photo by Eben Paxton.

emerging from the feather tracts by day 5 or 6, and feathers unsheathing on days 7 through 10. By days 10 or 11, nestlings are well feathered (with noticeable buffy wing bars), are able to perch on the edge of the nest and often actively preen. Wing flight feathers are unsheathed, although the tail is still very short and underdeveloped. By day 12, nestlings engage in much wing flapping in preparation for fledging and flight.

For the first few days after the chicks hatch, the female performs most of the care of the young. As the nestlings grow and demand for food increases, the male brings food to the nest more often and by days 8-10 both parents feed the young about equally. Only the female broods the young, although both parents will shade nestlings if the nest is exposed to full sun. McCabe (1991) presents many details of parental care in willow flycatchers (*E.t. traillii*). Nest attendance decreased with nestling age, with females spending less than 10 percent of their time at the nest after day 7. The number of feeding trips peaked at approximately 30 trips per hour during days 5 through 10.

Young willow flycatchers usually leave the nest (fledge) at 12 to 15 days of age, but will fledge prematurely as early as day 10 if a nest is disturbed (e.g., by a predator or researcher). After fledging, young flycatchers stay close to the nest and each other for 3 to 5 days. Recently fledged birds may repeatedly return to and leave the nest during this period (Spencer et al. 1996), up to three times per hour (McCabe 1991). Fledglings stay in the natal area a minimum of 14 to 15 days after fledging, possibly longer. Male and female adults both feed the fledged young, which beg loudly (typically a "*peep*" call) as they perch or move about in the dense vegetation. The period following

fledging is a time of high energy demand for fledglings, and parental feeding rates can be as high as 30 nest visits per hour.

Renesting

Second clutches within a single breeding season are uncommon if the first nest is successful, though this may vary between sites and years. M. Whitfield (unpublished data) has recorded only 5-10 percent renesting following successful first nesting. Most attempts at double brooding occur if the young fledge from the first nest by late June or very early July. On the other hand, willow flycatchers usually attempt another nest if the first nest is lost or abandoned due to predation, parasitism, or disturbance. Replacement nests are built in the same territory, and may be close to (even in the same plant) or far from (up to 20 m) the previous nest (McCabe 1991, Sogge et al. 1997b). McCabe (1991) found no differences in nest placement parameters between first nests and renests in *E.t. traillii*. Females usually begin construction of replacement nests within a day or two following the loss of the first nest, and replacement nests are usually constructed more quickly than first nests. Replacement nest building and egg laying can occur (uncommonly) as late as late-July or early August. Pairs may attempt a third nest if the second fails (Sferra et al. 1997, M. Whitfield pers. comm.), and Harris (1991) documented one female attempting six nests in one season. Clutch size (and therefore potential productivity) generally decreases with each nest attempt (Holcomb 1974, McCabe 1991, Whitfield and Strong 1995).

Post-Breeding Dispersal

Few specifics are known about when breeding pairs and their young leave their territory after nesting is completed. Adults that are successful in raising young may remain at breeding sites through mid-August and early September. Pairs with unsuccessful first and/or second nests sometimes abandon their territories midway through breeding season. In at least four cases, members of unsuccessful pairs have moved to other breeding sites within the same season and made second breeding attempts with new mates (Whitfield 1990, Paxton et al. 1997, M. Whitfield unpublished data). In Arizona, unmated males remained on territory through the early part of the breeding season but left by mid-July (Sogge 1995, Sogge et al. 1997b). The exact departure dates of most flycatchers are unknown, and it is not known if post-breeding flycatchers immediately begin their southward migration, or if they disperse and explore local riparian systems prior to heading south.

Competitors

In order for competition to occur, two or more species must attempt to utilize the same limiting resource (Lack 1954, Schoener 1982, Rosenberg et al. 1982). Individuals of the same species are often assumed to be competing (intraspecific competition), at least to some degree, particularly if they establish and defend separate breeding territories. Limiting resources are usually assumed to be food, nest sites, and/or mates. Interspecific competition should be strongest between closely related species that utilize resources in similar ways.

Empidonax flycatchers are very similar in morphology and food habits, and so present the most potential as competitors. Several studies suggest this may be the case. McCabe (1991), for example, found that willow and alder flycatchers maintained mutually exclusive territories at his study site in Wisconsin. Frakes and Johnson (1982) found similar diet and foraging behavior, and little territorial overlap, between coexisting willow and western (*Empidonax difficilis*) flycatchers in Washington. Johnson (1963) noted interspecific territoriality among *Empidonax* species, as did Beaver and Baldwin (1975). In the Southwest, however, the willow flycatcher is usually the only *Empidonax* flycatcher breeding within the dense riparian habitats that it favors, and no evidence has been seen of competition with other flycatchers.

Other less closely-related bird species are less likely to be significant competitors, even where they may share some ecological characteristics (such as nest placement or dietary overlap). McCabe (1991) found no evidence of intraspecific competition between willow flycatchers and co-occurring species such as yellow warblers (*Dendroica petechia*) and American Goldfinches (*Carduelis tristis*), which utilize similar habitat and resources.

There is little evidence that food is a limited resource at southwestern willow flycatcher breeding sites (although food availability may play a role in breeding site selection). For example, insects are usually abundant in flycatcher breeding patches, and nestling starvation is rarely recorded in unparasitized nests. Furthermore, willow flycatchers are to a large degree dietary generalists, and can select among differing prey types depending upon availability. Thus, although flycatchers share their breeding habitats with many other insectivorous birds, competition for food is probably negligible.

In terms of nest site competition, willow flycatchers can build nests in a variety of substrates and locations where suitable branching structure occurs. Several other birds, including yellow warblers and yellow-breasted chats (*Icteria virens*), occur in flycatcher sites and sometimes build nests of similar structure and placement. However, these species do not exclude

willow flycatchers from their territories (based on many examples of overlapping territories), and suitable nest sites are usually abundant and unlikely limiting, so competition is not likely.

The one resource for which evidence suggests possible intraspecific competition is mates. Male willow flycatchers are strongly territorial, and establish and defend territories through singing and aggressive interactions. At many southwestern willow flycatcher breeding sites, some territorial males fail to secure mates (Whitfield and Enos 1998, Ahlers and White 1999, Paradzick et al. 1999). This implies that females may be limited in some breeding groups, and that males are competing for this reproductively critical resource, with some males more effective than others. On the other hand, at several of these same sites, some males are polygynous and mate with more than one female in their territory (Whitfield and Enos 1998, Paradzick et al. 1999). The criteria and mechanism by which females evaluate and select males are unknown, but could include song (form, rate, volume, etc.), aggression, or other factors. Females may also be selecting a patch of habitat or breeding territory, whereby the male at that location becomes her mate by default.

Predation and Predators

Predation, particularly during the nesting phase, is a significant factor in the natural history and population dynamics of most small birds, and the southwestern willow flycatcher is no exception. Being a small bird with an open-cup nest, flycatchers are exposed to a wide suite of potential predators. In fact, predation can be the single largest cause of nest failure in some years (e.g., Whitfield and Enos 1996, McCarthey et al. 1998, Paradzick et al. 1999), and most of what we do know about predation and flycatchers involves nest predation. Predation events on adults of most passerine birds are rarely observed, and we have virtually no data of this kind for the southwestern willow flycatcher.

Potential predators observed at or near willow flycatcher territories include a variety of snakes, and small and mid-sized mammals such as chipmunks, weasels, raccoons, foxes, and domestic cats (McCabe 1991, Sogge 1995, Langridge and Sogge 1997, Paxton et al. 1997, Sferra et al. 1997). Predatory birds such as corvids (jays, crows and ravens), hawks (especially accipiters), and owls are regularly found in occupied flycatcher habitat. Brown-headed cowbirds, found in virtually every known flycatcher breeding site, effectively function as predators when they remove a flycatcher egg during parasitization events. Cowbirds have also been documented killing nestling Kentucky warblers (*Oporornis formosus*; Sheppard 1996) and other small songbird chicks (Tate 1967, Beane and Alford 1990, Scott and McKinney 1994), and may be acting as predators on southwestern willow flycatcher chicks (M. Whitfield and Arizona Game and Fish Department unpublished data).

There are four documented cases of nest predation on willow flycatchers. In Wisconsin, McCabe (1991) captured a milk snake (*Lampropeltis triangulum*) that was being harassed by adult willow flycatchers and found it had eaten a complete clutch of four eggs. Paxton et al. (1997) reported two predation events in Arizona. In one, a common king snake (*Lampropeltis getulus*) ate two nestlings, while a third survived by jumping out of the nest. At a second nest, an adult Cooper's hawk (*Accipiter cooperii*) took two nestlings (one at a time) from a nest. As with the king snake event, one nestling survived by jumping from the nest. At the Gila River in New Mexico, three nestlings were taken from the same nest by a Great Horned Owl (*Bubo virginianus*; S. Stoleson unpublished data).

Parasites and Disease

Although individuals of virtually all natural bird populations are exposed to diseases and are hosts to one or more species of internal or external parasites, little is known regarding the role of disease and parasites on most species or populations. Historically, avian parasite and disease literature focused only on documenting occurrence and development of host lists. Recently, increasing attention has been focused on the ecology of bird-parasite interactions (e.g., see Loye and Zuk 1991). Disease and parasites clearly may become a significant factor in periods of environmental stress, during particular portions of a life cycle, or if an exotic/introduced parasite or disease is introduced into a new or naive host (Karstad 1971, Atkinson and van Riper 1991, van Riper 1991). It remains difficult, however, to determine the effect of most parasites on most host species.

The willow flycatcher is host to a variety of internal and external parasites. Bennett et al. (1982) listed *E. traillii* as host for blood parasites such as *Haemoproteus*, *Leucocytozoon*, *Microfilaria* and *Tyrpanosoma*. Boland et al. (1989) and Sabrosky et al. (1989) recorded blow fly (*Protocalliphora* sp.) larvae on nestling willow flycatchers. Pence (1975) reported Traill's flycatcher as host to two species of nasal mites. Most, if not all, avian species (including *Tyrannid* flycatchers) are susceptible to viral pox (Karstad 1971), therefore this disease probably occurs in willow flycatchers (though specific records could not be found). Although these sources provide information on the identity and occurrence of parasites in willow flycatchers, there is no information on what impact, if any, parasites have on the infected birds. McCabe (1991) identified mites

(*Ornithonyssus sylviarum*) in 43 percent of flycatcher nests, but noted no obvious impairment of young. He also recorded blowfly larvae in 32 percent of nests, but again found no evidence of negative effects to nestling flycatchers.

There is virtually no published information available on diseases or parasites in the southwestern willow flycatcher. Recent preliminary examination of blood samples (C. van Riper and M. Sogge, unpublished data) found that *E.t. extimus* is host to several blood parasites, including *Haemoproteus* sp., *Leucocytozoon* sp., and *Plasmodium* sp. (avian malaria). As with other parasites, nothing is known regarding the ecological effects of these blood parasites on the willow flycatcher.

Data Needs

Although the southwestern willow flycatcher received relatively little research attention prior to 1990, a number of studies and monitoring programs initiated since that time have provided us with much useful information relative to the basic ecology of the flycatcher. New studies are being initiated every year. Research programs at the Kern River Preserve (CA), Roosevelt Lake and San Pedro River (AZ), Lower Colorado River (AZ, CA, NV, UT), Rio Grande (NM), and the Gila River (NM) are expected to continue for several more years and will yield valuable data on long-term patterns. Thus, while we have learned a tremendous amount in the last 10 years, we are positioned to discover even more during the next few years.

Unfortunately, there are still large gaps in our knowledge and understanding of southwestern willow flycatcher ecology, including many topics of considerable management and conservation interest (refer to the Research Needs chapter for a more complete listing of research needs and priorities). We need more precise delineation of the subspecies' northern range boundary, based on morphological and genetic examination of breeding populations. Another issue of key importance is the relative suitability of the native and exotic riparian habitats where flycatchers breed. More information is needed on how breeding patch size, shape, and landscape features are related to flycatcher breeding site selection and success. We lack an understanding of how microclimate characteristics influence breeding and nest site selection, especially in low and mid-elevation riparian areas. Data on nest predators are scant even though nest predation may be responsible for the majority of lost productivity. We know very little about the details of and mechanisms behind flycatcher breeding site selection, site fidelity, dispersal, and post-breeding movements, yet these are critical aspects of the flycatcher's habitat use and metapopulation dynamics. Hopefully, future research will be directed at these and other important questions.

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