

WILLOW FLYCATCHER USE OF IRRIGATION-FED WETLANDS IN THE FOOTHILLS OF THE SIERRA NEVADA OF CALIFORNIA

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Abstract.—Across California, Willow Flycatchers (*Empidonax traillii*) have been consistently and dramatically declining for decades. Fewer than 500 breeding pairs remain in the state despite the species being common and widespread less than a century ago. The species is extirpated from most of its historic range within California. Substantial conservation efforts have been made in the only known remaining strongholds of the species; mid-elevation Sierra Nevada meadows and riparian corridors of southern California. Previous reports, however, of Willow Flycatchers displaying territorial behaviors in irrigation-fed wetlands in low elevation areas of the Sierra Nevada foothills suggest additional areas may be either migratory stopover or breeding habitat. We followed up on prior anecdotal observations of Willow Flycatchers from the Sierra Nevada foothills, with the goal of confirming presence and meaningful use of the habitat. We detected flycatchers at nine of 14 wetlands surveyed and observed behaviors such as singing, counter-singing, and aggressive actions between individuals. Whether used as migratory habitat or breeding grounds, our observations demonstrate that Willow Flycatchers use irrigation-fed wetlands and continued management of these wetlands may be influential in the continued persistence of Willow Flycatchers in California.

Key Words.—breeding; *Empidonax traillii*; endangered species; small wetland; stopover

INTRODUCTION

As late as the 1940s, Willow Flycatchers (*Empidonax traillii*) bred across California, from sea level to around 2,400 m elevation and were commonly observed anywhere riparian scrub existed in the state (Grinnell and Miller 1944). Since then, the range of Willow Flycatchers in California has been reduced to only a few small pockets scattered across montane meadows of the northern Sierra Nevada and riparian corridors in southern California (Harris et al. 1987; Small 1994; Mathewson et al. 2013; U.S. Fish and Wildlife Service 2017), although it is a wide-spread and common migratory bird in North America (Sedgewick 2020). Where Willow Flycatchers persist in California, most populations continue to decline, with fewer than 600 breeding pairs remaining in the state (Loffland et al. 2014; U.S. Fish and Wildlife Service 2014). A few populations may be stable, however (Mary Whitfield, unpubl. data). The species is listed Endangered by California (California Department of Fish and Wildlife 2017). As such, all California populations are of conservation interest and identifying specific causes for their decline is critical.

Most historical declines are attributed to the widespread conversion of wetland habitat in California to agriculture (both cropland and wildland grazing) and urbanization (Sanders and Flett 1988; Frayer et al. 1989; Green et al. 2003). The reasons for ongoing declines in minimally disturbed and restored breeding habitat, however, especially in the Sierra Nevada where water resources are relatively abundant, remain unclear

(Loffland et al. 2022). Significant efforts have been taken to improve and restore breeding habitat for Willow Flycatchers in known populations, and there are now numerous meadows and waterways seemingly suitable for flycatchers that remain unoccupied (Schofield et al. 2018; Campos et al. 2020; Loffland et al. 2022). Despite ongoing declines in occupancy, when last monitored in the early 2000s those flycatchers remaining in the Sierra Nevada had breeding success and juvenile survivorship comparable to that of other related passerine species (Vormwald et al. 2011).

Like most migratory passerines, Willow Flycatchers spend most of their lives away from their breeding grounds (Lynn et al. 2003; Koronkiewicz et al. 2006), so improvements in the quality and availability of breeding habitat alone may not be sufficient to arrest or reverse population losses. Willow Flycatchers apparently have high wintering territory fidelity and relatively strong migratory connectivity linking breeding and wintering habitats (Koronkiewicz et al. 2006; Paxton et al. 2011; Ruegg et al. 2021; Mary Whitfield and Justin Shuetz, unpubl. report), suggesting that population trends in discrete breeding populations could be driven by effects in their wintering range or along migratory routes. Other studies have noted that many of the threats to Willow Flycatcher populations in the western U.S. are related to wintering and migration habitat (Paxton et al. 2017; Mary Whitfield and Justin Shuetz, unpubl. report), and Willow Flycatcher mortality is known to be at its highest during migration (Sillert and Holmes 2002; Paxton et al. 2017). Willow flycatchers have been found to maintain

ecologically unique resource, fed largely by irrigation water from cattle ranching or other human activities (Huntsinger et al. 2017; Van Schmidt et al. 2021). Foothill wetlands are typically small (< 1 ha), and relatively sparsely distributed within a semi-arid matrix of oak savannah, open ranch land, and scattered development. Irrigation systems in the Sierra Nevada foothills are extensive and were initially established in the mid-1800s during the California gold rush (Van Schmidt et al. 2021). In contrast with much of the rest of California, the number of small wetlands has been increasing over time as more irrigation water is introduced to the landscape (Van Schmidt et al. 2021). Although the majority of wetlands in the study region are on private land, there are also many wetlands located on public land. For public wetlands, irrigation water is often explicitly designated for conservation efforts rather than commercial activities like ranching (Van Schmidt et al. 2021).

Field methods.—At the outset of this study, we compiled incidental Willow Flycatcher observations made by the UCB rail surveyors between 2016 and 2019 to help select wetlands for Willow Flycatcher surveys in 2021. Willow flycatcher records included both direct in-the-field observations made by UCB surveyors and recordings made using audio recording units. We only considered records that included the diagnostic the fitz-bew vocalizations characteristic of Willow Flycatchers as positive observations because it is difficult (or sometimes impossible) to differentiate this species from other closely related flycatchers by sight alone. UCB conducted rail surveys at between 225 and 275 wetland patches in the Sierra Foothills annually, 34 of which had positive Willow Flycatcher detections (Fig 1). Observations at six of these locations occurred during what is considered peak breeding season for Willow Flycatchers in the Sierra Nevada, between June 15 and July 15 (Bombay et al. 2003). Because these detections were incidental and not a part of standardized surveys, we did not incorporate these observations into statistical analyses.

Wetlands surveyed by UCB between 2016 and 2019 were selected for their suitability as Black and Virginia rail habitat, which is typified by open areas of rushes (*Juncus* spp.), cattails (*Typha* spp.), or sedge (*Carex* spp.). Wetland patches dominated by riparian shrubs, the habitat overwhelmingly favored by Willow Flycatchers, were not actively surveyed by UCB, and Willow Flycatcher observations made by UCB were typically at the periphery of their study areas. Because areas of riparian shrubs were generally not surveyed by UCB, in addition to targeting Willow Flycatcher surveys within appropriate habitat at wetlands with confirmed flycatcher observations, we also identified nearby wetlands that were not surveyed by UCB but had a high density of riparian shrubs suitable for flycatchers. We selected 14 priority wetlands and established survey points within those wetlands for Willow Flycatcher

surveys (Fig. 1). Survey points were located 50 m apart within wetland habitat and excluded from surrounding matrix habitat types. We selected 10 sites based on their proximity to previous flycatcher detections and four sites based on a qualitative assessment of habitat characteristics by experienced surveyors. Nine of the 11 wetlands previously surveyed by UCB had regular Black Rail detections. All survey sites were located on public land; 12 of the wetlands were within the Spenceville Wildlife Area owned and managed by the California Department of Fish and Wildlife (CDFW), one was along a public road, and one was at a water treatment plant.

We followed survey protocols described by Bombay et al. (2003) that use broadcasts of Willow Flycatcher vocalizations to elicit a response from nearby flycatchers. Surveys took place between 19 May and 17 July 2021; an interval that spans the majority of the breeding season within the Sierra Nevada region. We visited sites 1–9 times during that time span (mean = 3.3 visits), depending on detections, activity, and the assessment of an experienced surveyor on habitat suitability (Appendix Table). In California, both territorial and migratory individuals may be present between mid-May and mid-June (Bombay et al. 2003; Sogge et al. 2010). Depending on previous detections at a site, site characteristics, and subspecies, individuals displaying territorial behaviors between late-June and mid-July are more likely to be resident breeding birds (Bombay et al. 2003; Sogge et al. 2010). The phenology of Willow Flycatchers encountered in the foothills may be different from that of Willow Flycatchers that breed at mid and high elevations of the Sierra Nevada (Bombay et al. 2003), so we cannot confidently confirm breeding status based on the timing of observations alone.

In the nearest breeding habitat to the Sierra Nevada foothills, 15 June marks the point in which territorial singing decreases and is the initial date in which breeding status may be suspected in instances where previous observations were made during that season (Bombay et al. 2003). In the southern population, breeding status may first be suspected starting 1 June, assuming previous observations (Sogge et al. 2010). We used this timing to define a period between 15 June and 15 July that would indicate evidence that a wetland represents breeding habitat; however, due to the unknown phenology of these individuals, we did not consider any of these detections to be confirmation of breeding status. Breeding status would not be confidently inferred until a detection after 24 June in the southern population and 26 June in the Sierra Nevada population (Bombay et al. 2003; Sogge et al. 2010). Following the Sierra Nevada protocol, an individual detected between 15 and 25 June, but not detected after, would not necessarily be considered a migrant or otherwise absent because detection probability falls substantially due to reduction in singing rates post-25 June (Bombay et al. 2003).

Each day broadcast surveys began 30 min before local civil sunrise and continued until 1000. This interval maximizes detectability due to Willow Flycatcher activity. Upon arrival at a wetland, surveyors spent 10 min passively listening prior to beginning broadcast surveys. After this, surveyors spent 6 min at each pre-defined point alternately playing Willow Flycatchers vocalizations and listening for responses. Broadcast survey points covered the full extent of the available habitat within a wetland and were spaced approximately 50 m apart to maximize detection probability. We delineated broadcast points before the initiation of surveys based on satellite imagery, although we moved or added points during initial survey visits if needed to fully cover available habitat.

If one or more Willow Flycatchers were detected (or suspected but unconfirmed) during broadcast surveys, a follow-up survey was conducted either immediately after broadcast surveys or the following day. The goals of follow-up surveys were to: (1) relocate any birds detected; (2) confirm the bird species identification by listening for the characteristic vocalizations if necessary; (3) identify feeding perches, singing perches, and other areas of use; (4) watch for behaviors indicative of breeding such as carrying nesting material, carrying food or fecal sac, and interacting with possible mates; and (5) locate nests or fledglings if possible. If the breeding status of the individuals observed remained inconclusive, additional follow-up visits were conducted when possible. During both initial broadcast surveys and follow-up surveys, experienced surveyors recorded individual behavior and interactions. We considered non-agonistic interactions featuring quiet vocalizations characteristic of pair-bonding as evidence of opposite-sex pairs.

We characterized the dominant vegetation and hydrology at each wetland within the study once per season while consulting aerial imagery as described in Bombay et al. (2003). Site-scale vegetation data collected during surveys included overall percentage of the wetland covered with riparian deciduous shrub (RDS), rushes, forbs, and grasses, and percentage RDS comprised of willows (*Salix* spp.; Bombay et al. 2003). Surveyors also noted whether signs of American Beaver (*Castor canadensis*) were observed within the wetland and whether the water source was natural or not.

We compared percentage saturated soil, percentage cover RDS, percentage cover grass, and percentage cover forbs of occupied versus unoccupied wetlands at sites surveyed for Willow Flycatchers using call-playback surveys using a Student's *t*-test and compared water source and apparent beaver presence using a Chi-square test. To meet parametric assumptions, we used the natural log transformation for percentage saturated soil, percentage cover RDS, and percentage cover forbs. Due to non-normality of data, we used a Mann-Whitney U-test to compare percentage cover of rushes and percentage RDS willow. Analytical methods such as Occupancy Models (Mackenzie et al. 2002) were inappropriate for this small dataset and would require further survey effort. We considered all results to be significant at a Bonferonni-corrected α -level of 0.00625. We report all values as the mean \pm standard error.

RESULTS

We recorded 17 separate detections of Willow Flycatchers at nine of the 14 wetlands surveyed (64%), with singing observed at seven of these locations (50%);

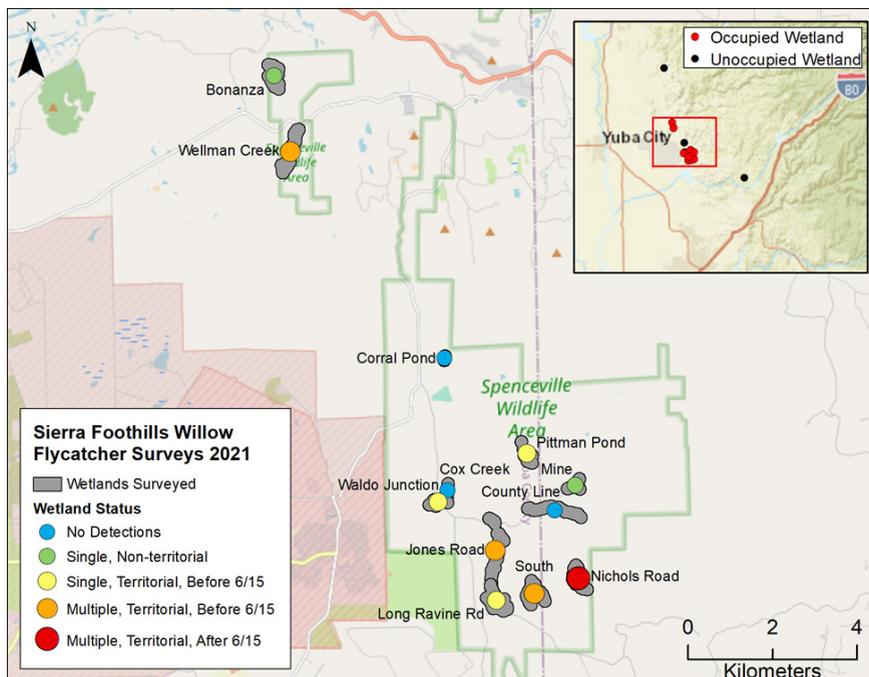


FIGURE 2. Location of wetlands in the Sierra Nevada foothills, including number, type, and timing of detections.

Fig. 2; Appendix Table). Five of the wetlands occupied by singing flycatchers (36%) had more than one individual detected on the same survey date and these individuals were observed interacting with one another (Appendix Table). The observations of Willow Flycatchers made at eight of nine occupied wetlands all took place prior to 15 June, the expected start of territoriality and breeding in nearby populations. One pair of Willow Flycatchers was observed on 15 June when Sierra Nevada Willow Flycatchers would be considered to be on their breeding territories, providing some evidence of a breeding attempt. This pair was observed singing and interacting with one another, which also typically indicates territoriality; however, there was no direct confirmation of a nest or young and no Willow Flycatchers were observed during surveys conducted after 15 June, so we could not conclusively ascertain breeding status.

In the majority of the wetlands where Willow Flycatchers were observed ($n = 8$), the flycatchers were detected on a single occasion. In the largest wetland in our study area (Wellman Creek), however, multiple individuals were observed interacting and displaying territorial behaviors during three separate survey visits. In early June the beaver dam that maintained the wetland broke, and the habitat quickly desiccated. After 12 June, Willow Flycatchers were no longer detected. Another of the wetlands where Willow Flycatchers were present (Bonanza) became dewatered early in the season due to the failing of the irrigation systems that typically feed the wetland. At the time of the initial visit to each wetland in early May, an average of 30.2% (± 4.88) of the total wetland area was inundated. In addition to these dewatering events, due to drought conditions in 2021; all wetlands were drier than they would be in typical years. The nearby Yuba River Marysville USGS water gauge recorded a mean annual flow rate in 2021 that was 23% of the historical 1970–2000 average annual flow (U.S. Geological Survey 2022). Habitat characteristics were similar between the nine occupied and five unoccupied wetlands (Table 1).

DISCUSSION

Our systematic surveys confirmed Willow Flycatcher presence in nine of 13 surveyed low-elevation wetlands in the Sierra Nevada foothills during late spring and early summer, demonstrating that the wetlands we surveyed are at a minimum extensively used by Willow Flycatchers during the migratory phase of their life cycle. Our observations also provide evidence (though not conclusive proof) that the wetlands surveyed may also represent breeding habitat. Further investigation will be necessary to identify the extent to which Willow Flycatchers use and rely on wetlands in the Sierra Nevada foothills, but we have confirmed that wetlands in the Sierra Nevada foothills provide resources to this species, whether used for breeding and migration or migration alone. The timing of the presence of Willow Flycatchers in our study suggests that these wetlands may serve as a stopover site for populations breeding either at higher elevation regions of the Sierra Nevada or further north. The mean arrival date for flycatchers detected in the mid and high-elevation Sierra Nevada (Bombay et al. 2003) and northern populations (<http://www.ebird.org>) corresponded to reduced detections at our foothill sites. Genetic sampling or tracking efforts may make it possible to identify which breeding population these individuals come from and could even provide evidence as to whether they represent a distinct population. There may be limited ability to differentiate breeding populations of Willow Flycatchers in western North America, however (Ruegg et al. 2021).

Managing wetlands to meet Willow Flycatcher needs in the Sierra Nevada foothills could be beneficial to Willow Flycatchers regardless of their breeding status, as both breeding and migratory stopover require similar habitat (Sedgewick 2020). Willow flycatchers historically nested in this region (Grinnell and Miller 1944), and with proper management preventing dewatering until after the breeding season, foothill habitats might once again provide opportunities for dispersing Willow Flycatchers

TABLE 1. Statistical tests comparing habitat characteristics of wetlands occupied by Willow Flycatchers (*Empidonax traillii*) with those not occupied by Willow Flycatchers. Significance based on a Bonferonni-corrected α -level of 0.00625. The abbreviation RDS = riparian deciduous shrubs and df = degrees of freedom. Numbers are means \pm standard error.

Habitat Covariate	\bar{x} Occupied	\bar{x} Unoccupied	Test Statistic	df	P-value
% Saturated Soil	26.7 (± 8.53)	38.0 (± 14.23)	$t = 1.12$	11	0.298
% Cover RDS	31.1 (± 7.16)	30.5 (± 10.08)	$t = -0.24$	11	0.818
% Cover Grass	29.8 (± 3.24)	32.0 (± 5.65)	$t = 0.64$	11	0.733
% Cover Juncus	14.6 (± 2.75)	3.0 (± 2.68)	$U = 3.50$	—	0.030
% Cover Forbs	8.7 (± 2.90)	14.8 (± 5.74)	$t = 0.56$	11	0.600
% RDS Willow	71.6 (± 10.7)	75 (± 14.8)	$U = 22.0$	—	0.587
Beaver Presence	3/9	1/4	$X^2 = 0.09$	1	0.764
Natural Water Source	5/9	3/4	$X^2 = 0.44$	1	0.506

originating in other portions of its range. Although the Sierra Foothills are hotter and drier than the area currently inhabited by the Sierra Nevada population, Willow Flycatchers have the evolutionary potential to use and adapt to hotter climates if other habitat parameters are suitable (Forester et al. 2023; Schofield et al. 2023).

Currently, the wetlands in our study area are primarily managed to support rail species, especially the Black Rail which, unlike the shrub-associated Willow Flycatcher, requires open habitat dominated by sedges and rushes (Richmond et al. 2010). A management approach that supports both species would also be beneficial to other meadow-associated animals. Historically, wetlands in the Sierra Foothills typically contain a mix of cover types (van Schmidt et al. 2021) and encouraging that heterogeneity could help promote wetland ecosystem health as a whole. Water availability is the most important factor in maintaining appropriate habitat for both Black Rails (Richmond et al. 2010) and Willow Flycatchers (Mathewson et al. 2013). Artificial irrigation is a primary strategy for providing water to wetlands in this region (Huntsinger et al. 2017; Van Schmidt et al. 2021), mimics historic conditions, and could benefit both species. Although most management and restoration activities have occurred on public land, water use and management in California is complex and involves many different stakeholders on private land and industry that have differing needs for water (Huntsinger et al. 2017; Van Schmidt et al. 2021). Another strategy for maintaining water on the landscape with or without supplemental irrigation could be encouraging beaver presence, which would benefit both Black Rails and Willow Flycatchers by retaining water later into the dry season. As we observed in the Wellman Creek site, the wetland became rapidly dewatered and transitioned to unsuitable habitat after the loss of a beaver dam.

The drought conditions experienced across California in 2021 (Seager et al. 2022), combined with the abrupt loss of existing water at the locations maintained by beaver dams and irrigation, confound the interpretation of our observations. It is possible that these conditions prevented breeding or resulted in nest failures in locations that commonly support breeding Willow Flycatchers during more favorable years. Further investigation is needed to determine whether Willow Flycatchers use the Sierra foothills for breeding habitat and to what extent wetlands in the foothills are used during migration. Historically, the avifauna of the Sierra foothills has been relatively poorly studied; the extensive breeding population of Black Rails, for example, was not discovered until 1994 (Girard et al. 2010). We can reasonably suspect that if Willow Flycatchers were breeding in the central Sierra foothills, their phenology would be different from that of flycatchers nesting in the mid to high-elevation Sierra Nevada, where green-up is significantly later, and likely more similar to populations nesting in southern California (e.g., Kern River Valley).

Although formerly characterized by abundant wetland habitat, the Central Valley of California and the adjacent low-elevation portions of the Sierra Nevada foothills lost 86% of historical wetlands between 1936 and 1989 (Framer et al. 1989). Protecting and maintaining remnant wetlands is thus critical for species dependent on these habitats for migration and reproduction.

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HELEN (BOMBAY) LOFFLAND received her B.S. in Wildlife Biology from the University of California, Davis, and her M.S. in Biology from California State University, Sacramento. She has spent the last 20 y studying Willow Flycatchers and other meadow birds, raptors, carnivores, insects, plants, and fish, primarily in the Sierra Nevada. She is particularly interested in the complex disturbance regimes and associated ecological relationships in Sierra meadows and for the last 12 y has worked on multi-species bird monitoring protocols for meadow restoration. She is now expanding her research into pollinator use of meadows and ephemeral riparian and upland habitats in post-fire landscapes. (Photographed by Helen Loffland).



KRISTEN HEIN STROHM earned her M.S. in Wildlife Biology from Colorado State University, Ft. Collins, and has over 20 y of professional experience as a Wildlife Biologist and Watershed Restoration Planner. Passionate about conservation and restoration, Kristen has developed the wildlife science components of more than 10 multi-species habitat restoration plans in northern California, and has performed hundreds of wildlife and vegetation surveys in a variety of ecosystems throughout the U.S. and Brazil. (Photographed by Stephen Hein).

APPENDIX TABLE. Survey dates and observations made during Willow Flycatcher surveys conducted in the Sierra Nevada foothills in 2021.

Site Name	Survey Date	Number of Willow Flycatcher Detected	Behaviors/Notes
Bonanza	May 19	0	
Bonanza	June 6	1	Foraging
Bonanza	June 24	0	
Bonanza	July 12	0	
Corral	June 2	0	
County Line	May 23	0	
County Line	June 22	0	
Cox Creek	July 6	0	

APPENDIX TABLE (CONTINUED). Survey dates and observations made during Willow Flycatcher surveys conducted in the Sierra Nevada foothills in 2021.

Site Name	Survey Date	Number of Willow Flycatcher Detected	Behaviors/Notes
Honcut Creek	June 10	0	
Honcut Creek	June 20	0	
Jones Road	May 27	1	Singing Male
Jones Road	June 29	0	
Jones Road	July 8	0	
Jones Road	July 15	0	
Lake of the Pines	June 11	0	
Long Ravine	June 13	1	Singing Male
Long Ravine	May 25	0	
Mine	June 3	1	Singing Male
Mine	June 8	0	
Mine	July 17	0	
Nichols Road	June 5	0	
Nichols Road	June 15	1	Singing Male + Female
Nichols Road	June 26	0	
Nichols Road	July 7	0	
Pittman Pond	June 3	1	Singing Male
Pittman Pond	June 8	0	
Pittman Pond	July 1	0	
Pittman Pond	July 14	0	
South Site	May 28	1	Singing Male
South Site	June 19	0	
South Site	July 2	0	
South Site	July 15	0	
Waldo Junction	May 25	1	Singing Male
Waldo Junction	May 29	0	
Waldo Junction	June 16	0	
Waldo Junction	July 6	0	
Waldo Junction	July 18	0	
Wellman Creek	May 20	1	
Wellman Creek	May 24	1	
Wellman Creek	May 29	1	
Wellman Creek	June 1	2	Counter Singing Males
Wellman Creek	June 2	3	Counter Singing Males
Wellman Creek	June 12	1	Beaver Dam Broke
Wellman Creek	June 23	0	
Wellman Creek	July 3	0	
Wellman Creek	July 18	0	