SIERRA NEVADA WILLOW FLYCATCHER DECLINE CONTINUES BUT LOSSES ABATE AT TWO RESTORED MEADOWS

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ABSTRACT: Willow Flycatcher (*Empidonax traillii*) populations have been declining across the western United States for decades. The Sierra Nevada–southern Cascades population in California is especially vulnerable, with fewer than 200 pairs remaining. Hydrologic restoration has been recommended for conserving this population. Other riparian songbirds have increased in response to restoration, but little is known about how restoration has affected the Willow Flycatcher. The Little Truckee River has long been a stronghold for the Willow Flycatcher, and the demography of the population there was studied intensively from the late 1990s through 2010. Baseline data from that study provided an opportunity to gauge the species' response to pond-and-plug restoration projects completed at two meadows within the study area in 2009 and 2010. We aggregated and analyzed data from Willow Flycatcher surveys from 1997 through 2019 at the two restored meadows as well as nine nearby unrestored meadows with at least two Willow Flycatcher territories at some time during the demographic study. At most meadows, the number and density of Willow Flycatcher territories declined over the two-decade study period. However, losses at the unrestored meadows were significantly greater than at the restored meadows, where territory density clearly did not collapse following the disturbance caused by restoration and then remained largely stable thereafter. Within large meadows already occupied by Willow Flycatchers, meadow restoration that restores hydrologic function and increases flooding over creekbanks may be an effective strategy for stabilizing declining Willow Flycatcher populations in the Sierra Nevada.

Once abundant in nearly all shrubby riparian areas across the entire length and breadth of California below an elevation of 2500 m (Willett 1912, 1933, Grinnell and Miller 1944), the Willow Flycatcher (*Empidonax traillii*) now occurs only in small numbers, primarily at scattered meadows above 1200 m in the Sierra Nevada and southern Cascades and along a few waterways in the arid southwestern portion of the state. The species, including all subspecies, was designated as endangered in California in 1991 (CDFW 2021). In the Sierra Nevada and nearby southern Cascades in northern California, Willow Flycatcher populations include representatives of both subspecies *adastus* and *brewsteri* and potential hybrids (Paxton 2000) and are almost completely reliant for breeding habitat on mid-elevation wet meadows (Serena 1982, Harris et al. 1987, Sanders and Flett 1989, Bombay et al. 2003a, b, Mathewson et al. 2013, Schofield et al. 2018). Declines and local extirpations have continued for many decades throughout the region (Siegel et al. 2008, Mathewson et al. 2011, Loffland et al. 2014), where the species now persists at fewer than 100 meadows (Loffland et al. 2014; H. Loffland unpubl. data).

The Little Truckee River watershed and nearby locations in Sierra and

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Nevada counties represent one of only a few remaining strongholds for the species in California, with a cluster of meadows that collectively retained approximately 30 territories at least until 2000 (Mathewson et al. 2013). Within this cluster, along the Little Truckee River, Willow Flycatcher conservation has been a priority at the Perazzo Meadows complex (which comprises three large meadows, Upper Perazzo, Middle Perazzo, and Lower Perazzo) for nearly 40 years. The California Department of Fish and Wildlife and others surveyed these meadows for the Willow Flycatcher regularly through the 1980s and early 1990s (Serena 1982, Sanders and Flett 1989). Between 1997 and 2010 the meadow complex was the site of a long-term demography study supported by the U.S. Forest Service (Mathewson et al. 2011, 2013). Since 2011, The Institute for Bird Populations and its partners have continued to survey in most years, though effort has been reduced and less consistent than during the years the demography study was underway.

Upper Perazzo and Middle Perazzo were treated in the fall of 2009 and 2010, respectively, with the "pond-and-plug" technique (Wilcox et al. 2001, Hammersmark et al. 2008), a form of partial channel fill that can restore hydrologic functioning to meadows where channels are deeply incised, lowering the water table and desiccating the meadow. In pond-and-plug restoration the channel is partially filled by means of heavy equipment excavating portions of a meadow's existing stream channel and using the excavated material to build one or more semi-permeable "plugs" in the channel downstream from the excavation site(s). The plugs force flow into the historic channel or a newly engineered channel, capture sediment, and facilitate inundation of the excavated portions of the channel, which become "ponds" (Lindquist and Wilcox 2000, Pope et al. 2015). Pond-and-plug restoration is intended to enhance ecosystem services including flood attenuation, water storage, water quality, and carbon sequestration, as well as to foster biodiversity through habitat improvement (Hammersmark et al. 2008, Norton et al. 2011, Viers et al. 2013, Campos et al. 2020). At the same time the Forest Service also instituted a new rest-rotation plan to manage grazing (alternating years of grazing and rest) at the restored meadows. The plan's goals were to improve and protect vital wildlife habitat, with an emphasis on the Willow Flycatcher, Yellow-legged Frog (*Rana muscosa*), and Lahontan Cutthroat Trout (*Oncorhynchus clarkii henshawi*), and restore hydrologic function, improve water quality, and improve forage condition for livestock and wild ungulates.

At Upper and Middle Perazzo, pond-and-plug was implemented specifically to reconnect the water table within the meadow system to the meadow's floodplain, and to reverse the desiccation and loss of aquatic habitat that resulted from human-caused alterations of the natural stream channel. Anthropogenic degradation of the site traces back to the late 1800s when the Henness Pass road that parallels the meadow system, and crosses it in multiple locations, became a major route across the Sierra Nevada. At that time sheep and cattle grazed throughout the area, and early allotment documents reported that in 1907 the number of grazing animals was 5 times that using the allotment in the recent decades (Byrd 1992, Swanson Hydrology and Geomorphology 2008, USDA 2008). At the same time, Upper Perazzo was home to a dairy, and efforts to drain the meadow for better accessibility led to the primary channel of Perazzo Canyon Creek being actively re-routed.

The combination of stream re-routing, road construction, logging, mining, dairying, and livestock grazing curtailed the capacity of the stream system to water the meadow adequately.

Pond-and-plug or other partial channel-fill measures have been implemented at dozens of meadows across California's Sierra Nevada and southern Cascades in recent decades and have been shown to increase the species richness of meadow birds, especially when riparian shrubs were already extensive prior to restoration (Campos et al. 2020). However, the approach remains controversial because of its high cost, use of heavy equipment and major excavation, and creation of ponds that may spur other ecological changes or consequences, particularly at lower elevations where it may create habitat for the non-native bullfrog (*Lithobates catesbianus*; Pope et al. 2015). Moreover, although improvement or creation of habitat for the Willow Flycatcher is often explicitly invoked as a justification for ambitious meadow-restoration projects in the region, the flycatcher's response to pond-and-plug restoration has never been evaluated. We sought to assess the effects of pond-and-plug restoration at Upper and Middle Perazzo meadows on persistence of Willow Flycatcher territories at the restored meadows, using as reference sites nearby untreated meadows that Willow Flycatchers had also occupied. We considered the updated grazing plan at the treated meadows to be part of the overall restoration effort and did not attempt to tease apart effects of pond-and-plug restoration from changes in grazing management.

METHODS

Study Area

We included in our study area 11 meadows in and around the Little Truckee River watershed within the historic primary subsistence and settlement lands of the Washoe people, and currently in California's Sierra, Nevada, and Placer counties (Figure 1). These 11 meadows constitute all the sites in the local area known to have been occupied by at least two Willow Flycatcher territories during any breeding season since 1997. The meadows range in size from 15 to 161 ha and in elevation from 1736 to 2077 m above sea level (Table 1). Their grazing regimes have varied from meadow to meadow. They span four distinct grazing allotments (three for cattle, one for sheep), as well as ungrazed areas outside of the allotments. At the time the demographic studies began in 1997, five of the meadows were under private ownership and management, but all have since been acquired by local or federal agencies or are under conservation easements managed by nonprofit entities. Two of the meadows, Upper Perazzo and Middle Perazzo, underwent pond-and-plug restoration during the fall of 2009 and 2010, respectively (Figure 2).

We treated the numbers of territories at the 11 meadows as statistically independent because during the demographic study we observed a high rate of site fidelity of individual Willow Flycatchers in successive years, and only rarely observed movement of birds between meadows within a year. Between 1997 and 2010, 89% of 70 individually color-marked adults (but only 34% of 46 one-year-old adults) returned to the previous year's meadow (Mathewson et al. 2013). The mean distance of natal dispersal of one-year-olds that

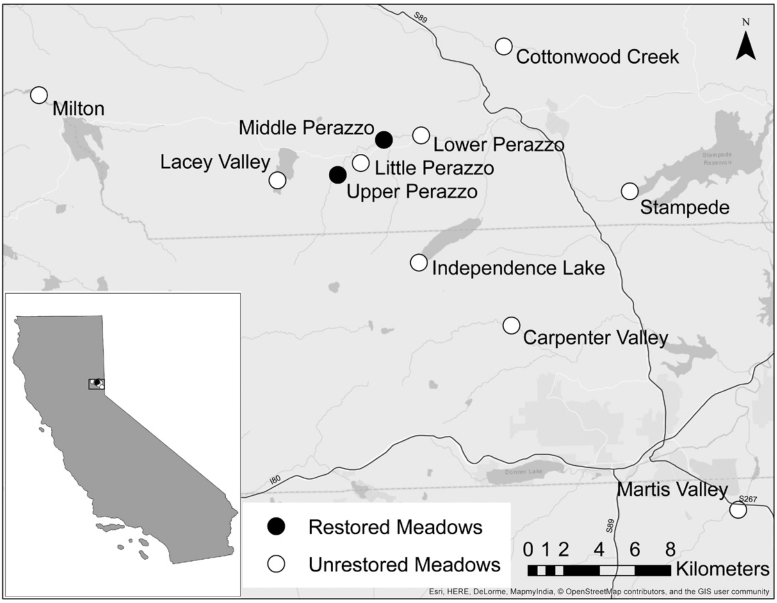

FIGURE 1. Meadows in the northern Sierra Nevada, California (inset), where surveyors used broadcast surveys and territory monitoring to assess the number of Willow Flycatcher territories annually from 1997 to 2019 (not all sites were surveyed during every year of the study). Upper and Middle Perazzo meadows underwent pond-and-plug hydrologic restoration during fall 2009 and 2010, respectively. Darker gray shading indicates water bodies.

dispersed away from their natal meadows was 8.36 ± 7.36 km (Mathewson et al. 2013). None of the 11 meadows was farther than 15 km from its nearest neighbor—a distance within the observed mean dispersal distance + 1 standard deviation, suggesting that all sites were equally available to the birds of this population.

The two restored meadows (Upper and Middle Perazzo) were not selected randomly from the 11 meadows in our study. The Tahoe National Forest chose them for restoration on the basis of important ecological benefits for a wide variety of aquatic and terrestrial plant and animal species as well as to benefit downstream water users by decreasing peak flows and extending the period over which water drains from the meadow. We had no control of which sites were restored, or when, and undertook our study because we had access to unprecedented baseline Willow Flycatcher data and saw the need for the restoration's effects to be assessed. Despite the lack of randomness in selection of restoration sites, we account for potential bias by including many times more reference sites than treatment sites and by ensuring that at the beginning of the study many of the reference sites had habitat and Willow Flycatcher densities similar to those of the restoration sites.

Table 1 Characteristics of Restored and Unrestored Meadows Assessed for Use by the Willow Flycatcher

Meadow	Total area (ha)	Extent of Willow Flycatcher habitat (ha)	Elevation (m)	Land manager[a]
Reference				
Carpenter Valley	86	69	1904	TNC[b]
Cottonwood Creek	17	17	1877	USFS
Independence Lake	20	20	2137	TNC[b]
Lacey Valley	161	101	2077	TDLT[b]
Little Perazzo	25	25	2015	USFS
Lower Perazzo	23	23	1987	TDLT
Martis	80	59	1772	USACOE
Milton	15	15	1736	USFS & private
Stampede	32	32	1814	USFS
Restoration				
Middle Perazzo	98	82	1978	USFS[b]
Upper Perazzo	105	85	1999	USFS

[a]TNC, The Nature Conservancy; USFS, U.S. Forest Service; TDLT, Tahoe Donner Land Trust; USACOE, United States Army Corps of Engineers.

[b]Privately owned at the start of the study in 1997, but subsequently acquired by a local agency or nonprofit organization.

Data Collection

We aggregated all Willow Flycatcher survey data from the 11 meadows that constitute our study area from 1997 through 2019. Over this 23-year period, the subset of meadows that was monitored varied from year to year with funding, changes in site ownership and access, and the project's annual objectives. Effort varied from surveying for Willow Flycatcher presence and monitoring territories throughout the breeding season at all meadows annually from 2003 to 2006 to no surveys in 2013 (Table 2). Although data-collection procedures varied through the study, we included only data collected through standardized broadcast surveys and territory monitoring.

Broadcast surveys. At most meadows each year's surveys began with two rounds of broadcast surveys that followed the standardized Willow Flycatcher survey protocol for the Sierra Nevada developed by Bombay et al. (2003a). In a few instances, a meadow received only one broadcast survey followed by repeated visits for territory monitoring (described below). More typically meadows were surveyed twice between 31 May and 25 July. The survey season was divided into three distinct periods that roughly coincide with the initiation of distinct phases of breeding: arrival and nest building (31 May–14 June), egg laying and incubation (i.e., peak breeding season; June 15–June 25), and chick hatching and fledging (26 June–25 July). One of the two surveys took place between 15 June and 25 June because this is when Willow Flycatchers are most likely to be actively singing and defending territories and are therefore most detectable and least likely to be passage migrants. The other survey took place either before or after the peak season, depending on

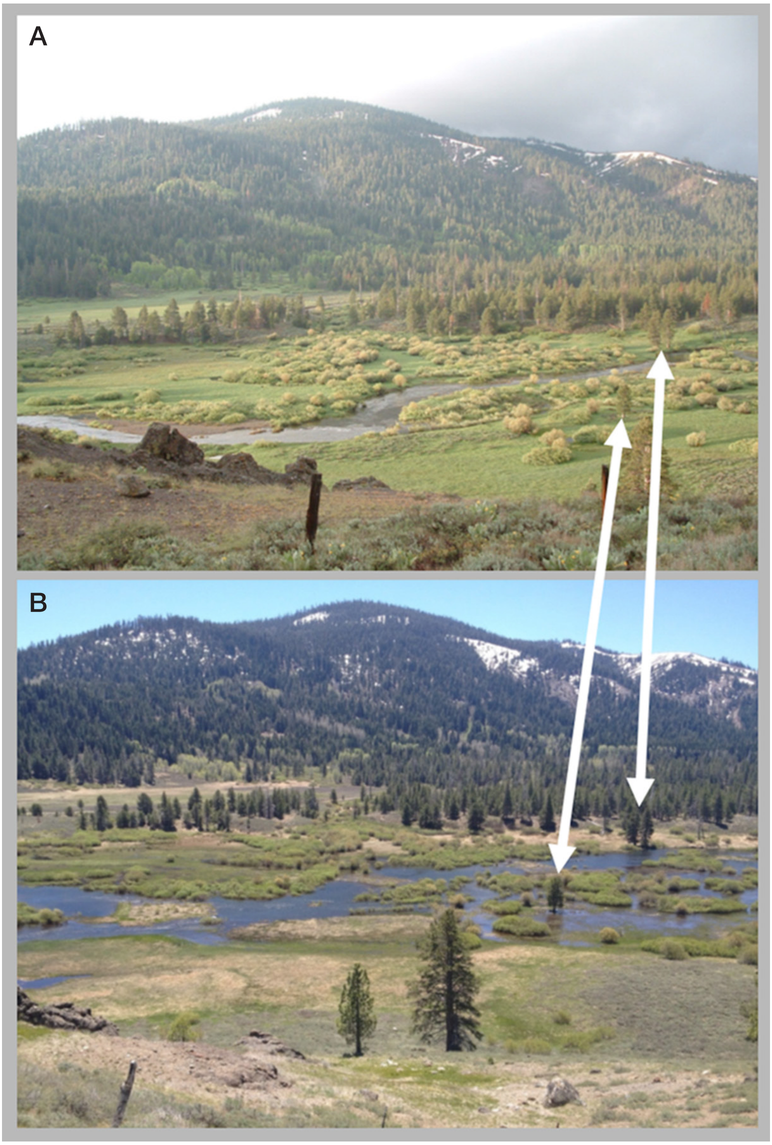

Figure. 2. Middle Perazzo Meadow in 2009 (A, one year prior to restoration and following a winter with 67% of the 50-year average annual snowpack; DWR 2021) and 2018 (B, 8 years after restoration and following a winter with 69% of the 50-year average annual snowpack; DWR 2021). White lines indicate reference trees visible in both photos. After restoration, note the more extensive flows over the streambanks during peak runoff.

Table 2 Number of Willow Flycatcher Territories Confirmed at Meadows Surveyed in the Sierra Nevada, 1997–2019[a]

	Meadow										
Year	Carpenter Valley	Cottonwood Creek	Independence Lake	Lacey Valley	Little Perazzo	Lower Perazzo	Martis Valley	Middle Perazzo	Milton	Stampede	Upper Perazzo
Territories monitored throughout season											
1997	*	*	*	*	1	4	*	11	*	*	12
1998	7	*	3	12	1	4	*	13	*	*	9
1999	5	*	2	14	1	6	*	12	*	*	7
2000	4	*	3	12	0	4	*	9	*	0	5
2001	6	*	1	12	1	5	*	8	4	1	3
2002	6	*	3	7	1	4	*	10	3	1	2
2003	5	2	2	8	2	3	2	10	5	2	5
2004	6	2	2	9	2	3	3	8	5	1	4
2005	8	2	2	5	2	3	3	11	6	0	4
2006	5	5	3	5	1	4	1	9	6	1	11
2007	*	3	2	6	1	3	3	8	4	0	8
2008	*	2	2	3	1	1	3	6	4	1	8
2009	*	2	*	4	1	2	3	8	4	1	8
2010	*	1	*	*	1	2	2	6	2	1	8
Territory monitoring limited											
2011	*	*	*	*	*	1	*	*	*	*	4
2012	1	*	*	3	0	0	*	4	*	1	6
No surveys											
2013	*	*	*	*	*	*	*	*	*	*	*
Surveys only; no territory monitoring											
2014	*	1	*	1	0	0	0	7	2	3	7
2015	*	*	*	*	0	1	*	*	*	*	*
Territories monitored throughout season											
2016	0	1	3	1	*	0	0	8	*	*	6
2017	0	0	3	1	*	0	0	10	*	*	6
Territory monitoring limited											
2018	1	1	2	0	0	0	*	4	2	4	6
2019	0	0	*	0	0	0	*	7	*	1	4

[a]On basis of broadcast surveys and territory monitoring. Asterisks indicate years when a meadow was not surveyed or survey effort was insufficient to determine territory numbers.

conditions at the site. Surveys at any one meadow were always separated by at least 10 days.

Broadcast-survey stations were distributed across the full extent of available habitat (areas with willow or other deciduous riparian shrubs) within a meadow, spaced approximately 50 m apart. Survey stations were selected prior to surveys by GIS, but locations were sometimes adjusted in the field to cope with obstacles such as impenetrable vegetation or uncrossable streams.

Once stations were established during the first visit to a meadow, subsequent surveys in the same and following years were made the same locations if still accessible. Broadcast surveys generally began within 10 minutes of civil sunrise and concluded by 10:00. Upon arriving at a meadow, surveyors spent 10 minutes passively listening prior to beginning broadcast of Willow Flycatcher songs. At each survey station, surveyors spent a total of 6 minutes alternately playing Willow Flycatchers vocalizations and listening for responses. Although contact calls other than the diagnostic vocalizations or and visual observations and photographa were noted, we considered only characteristic “fitz-bew” or “zwee-oo” vocalizations sufficient for a positive identification, even by expert observers.

All the stations at smaller meadows were typically surveyed within a single morning, but larger meadows required multiple consecutive days for completion of a survey.

Territory monitoring. In some instances, surveyors monitored a territory by a modified version of the protocols described by Bombay et al. (2003a). If at least one Willow Flycatcher (or a suspected but unconfirmed Willow Flycatcher) was detected during a broadcast survey, territory mapping originating at the location of the initial detection followed either immediately after the completion of broadcast surveys that day or within the next few days. Surveyors used a hand-held GPS to record coordinates of singing perches and foraging locations for the male (and female, if detected) while quietly observing behavior for approximately 30–90 minutes. Using GIS, we then mapped the polygons defined by these coordinates to help determine the number and position of territories. The initial territory-mapping visit and all subsequent territory-monitoring visits were intended to (a) relocate the bird(s), (b) confirm identification by listening for a “fitz-bew” or “zwee-oo” vocalization (if one was not heard during the original broadcast survey), (c) identify areas of use such as foraging and singing perches, (d) observe behavior to infer breeding status (e.g., carrying nesting material, carrying food or fecal sac, or interacting with mates), and (e) attempt to locate nests or fledglings. Each territory received multiple visits per season, usually at least once every 7 days (or more often if nests were being monitored). Territories were visited typically between 05:30 and 10:00 but were also surveyed opportunistically during other times of the day.

Data Analysis

We used the results from broadcast surveys and territory monitoring to determine the number of territories present at each meadow annually. Observations were considered to signify an occupied territory in a given year if a Willow Flycatcher was observed on at least two dates between June 15 and July 25, or if observed behavior confirmed attempted nesting (e.g., carrying nesting material or carrying food). When multiple Willow Flycatchers were singing in close proximity to one another, we determined the number of territories on the basis of observations of counter-singing between males and other territorial defense. We considered a singing male to indicate an occupied territory irrespective of whether it was paired. Although females are known to sing the diagnostic “fitz-bew” song occasionally, we considered singing birds to be male unless we had data or observations to suggest otherwise. From 1997 to 2010, many of the territorial birds were marked with color bands, which helped in this assessment, but by 2014 very few banded individuals remained, so after that sex determination had to be based on behavioral observations only.

We used linear regression models to examine trends in territory density (territories per hectare of suitable habitat available in each meadow) at the scale of the individual meadow. In this analysis we included only those years with Willow Flycatcher survey data, and we considered years with missing data to be null values. To account for multiple tests, we applied a Holm adjustment to probabilities generated by the linear models. We used territory density as our response variable to account for lack of normality in territory-count data and the effect of varying meadow size on the absolute numbers of territories possible at each meadow. We used ArcMap 10.14 to determine the area of each meadow suitable as a basis for our density estimate. We hand-digitized the boundary of each meadow as seen in color imagery generated 2009–2014 by the National Agricultural Imagery Program (visually delineating between meadow vegetation and the surrounding upland covered by forest or sagebrush) and eliminated any large (>5 ha) contiguous areas of open meadow that lacked deciduous riparian shrubs (based on vegetation visible in imagery and personal knowledge of each meadow). Then we calculated the area of the resulting polygons to represent the area of each meadow that provided the Willow Flycatcher's basic habitat: a mix of open meadow and large (>0.1 ha) patches of willow or other riparian shrubs (Table 1).

We then aggregated territory-density data for all meadows to assess the overall regional trend in the density of Willow Flycatcher territories through time. To avoid regional trend estimates being skewed because survey effort was less consistent in some years or meadows, we restricted the regional analysis to only those meadows and years without substantial missing data. We eliminated meadows that were missing data for more than two years between the completion of pond-and-plug restoration at Upper and Middle Perazzo and the end of our study in 2019 (Martis Valley, Milton, Little Perazzo, and Stampede). We then eliminated all data from years when more than one of the remaining 7 meadows was missing survey data (1997 and 2009–2015). This data filtering yielded 17 years of territory-density values for 7 meadows to be analyzed (n = 119). For the 9 site–year combinations in this reduced dataset for which data were still missing, we imputed the mean and replaced the missing values with the average territory density across all 7 meadows and 17 years (0.09 territories/ha; Pratama et al. 2016).

To assess the effect of the pond-and-plug restoration efforts on the Willow Flycatcher's population trends in the study area, we used a generalized linear mixed model (GLMM) in a "before, after, control, impact" (BACI) framework, with restoration status and time period acting as fixed effects and year, meadow, and their interaction terms acting as random effects. This framework makes it possible to distinguish population trends related to the restoration from background trends occurring independent of the restoration (Conner et al. 2016, Pardini et al. 2018). We considered the territory-density estimates in the restored Perazzo meadows to be the "impact" group and the remaining unrestored meadows to be the "control" group. The density estimates during the 13 breeding seasons leading up to the first restoration project (fall of 2009) made up the before-treatment group, and territory estimates during the nine breeding seasons after restoration was completed at the second project (fall of 2010) made up the after-treatment group. In addition to helping differentiate the effect of treatment from background trends, a GLMM accommodates the Poisson distribution of our data and is robust to some missing data, thereby allowing us to retain all meadow-by-year combinations in our analysis. We created these models in R statistical software version 4.1.0 with the function "glmer" in the package "lme4" (Lee et al. 2006, Bates et al. 2015, R Core Team 2017). We subsequently ran post-hoc pairwise interaction tests with the function "lsmeans" from the package "lsmeans" in R to examine the differences between individual pairs of variables. In these pairwise interaction tests we adjusted *p*-values by using the Tukey correction function.

RESULTS

The 11 meadows in our study area encompassed 846 stations for broadcast surveys for the Willow Flycatcher, at which 27,738 broadcast surveys were completed between 1997 and 2019. We used the results from these broadcast surveys plus additional observations during territory monitoring to determine the number of territories at each meadow in each year (Table 2) and calculate territory density. At six of the meadows the decline in the density of Willow Flycatcher territories during the study period was significant (Figure 3). The three meadows with the greatest declines (Lacey Valley: $R^2 = -0.875$, $p < 0.001$; Carpenter Valley: $R^2 = -0.749$; $p < 0.001$; Lower Perazzo: $R^2 = -0.835$; $p < 0.001$) each supported 0.1–0.25 territories per hectare at the beginning of the study period but were entirely vacant by the end. Although declines were not as severe at Middle Perazzo, Cottonwood Creek, and Martis Valley, they were still significant ($R^2 = -0.583$, $p < 0.001$; $R^2 = -0.456$, $p = 0.041$; $R^2 = -0.604$, $p = 0.012$, respectively). Territory density increased at one meadow (Stampede: $R^2 = 0.255$; $p = 0.180$), but that increase did not reach the level of significance. Territory density remained unchanged or declined non-significantly at four others (Independence Lake: $R^2 = 0.069$, $p = 0.813$; Little Perazzo: $R^2 = -0.047$, $p = 0.523$; Milton: $R^2 = -0.333$, $p = 0.145$; Upper Perazzo: $R^2 = -0.014$, $p = 0.813$). Though its trend did not qualify for statistical significance, Little Perazzo nonetheless retained no Willow Flycatcher territories by the end of the study period.

The overall density of Willow Flycatcher territories at the 7 meadows with the most robust survey effort over the study period declined significantly (Figure 4; $F = 37.88$, $R^2 = 0.25$, $p < 0.001$). This decline in density corresponds to an average loss of 0.004 territories per ha of meadow annually, amounting to 1.55 territories lost per year across the 7 meadows (397 ha of habitat vacated).

The GLMM revealed an overall significant difference in territory density among the four categories defined under the BACI framework ($t = -3.104$, $p = 0.0125$; Table 3). Pairwise comparisons show this difference is driven by a significant decline in territory density in the unrestored meadows between the pre-restoration and post-restoration periods (Table 4). No other differences in the pairwise comparisons were significant. The relative and absolute decline in territory density at the restored meadows was markedly lower than at the unrestored meadows (Figure 5). At unrestored meadows, the estimated

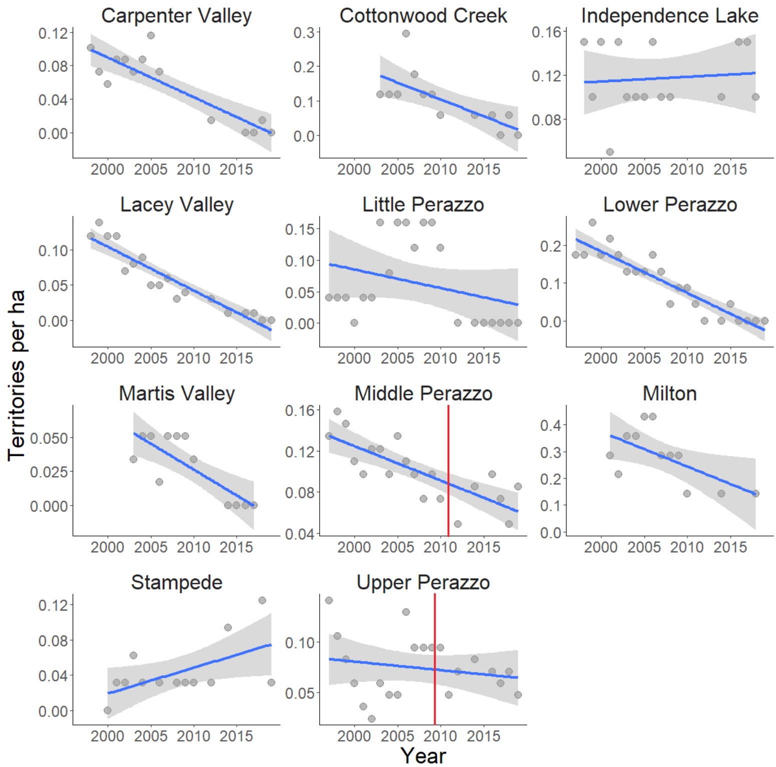

FIGURE 3. Trend in Willow Flycatcher density at the 11 meadows studied in or near the Little Truckee River watershed from 1997 to 2019. Blue lines indicate estimated trends and gray shading depicts the 95% confidence interval. Red vertical lines on the graphs for Upper and Middle Perazzo indicate when pond-and-plug restoration was implemented.

mean territory density declined 62%, from 0.12 to 0.05 territories per hectare, while territory density at restored meadows declined 20%, from 0.09 to 0.07 territories per hectare.

DISCUSSION

During this study, beginning in 1997, we observed a continued decline in Willow Flycatchers throughout our study area, mirroring trends across the Sierra Nevada and California Cascades. Threats facing the Willow Flycatcher are numerous, including intensifying droughts as well as possible habitat loss or degradation on the winter range and along migration routes (Green et al. 2003, Diffenbaugh et al. 2015, Paxton et al. 2017, Ruegg et al. 2018, 2021). The effects of these extrinsic factors may be exacerbated by population declines, as social cues needed for habitat selection may disappear (Schofield et al. 2018),

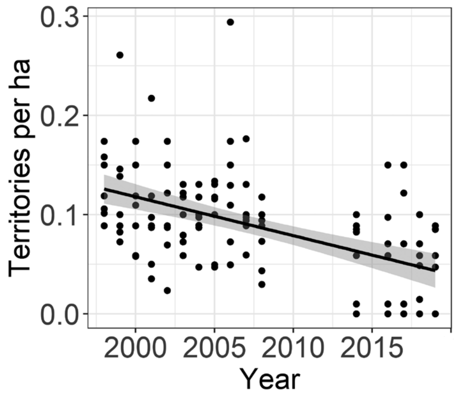

Figure 4. Combined density of Willow Flycatcher territories at 7 meadows with robust survey data in and near the Little Truckee River watershed from 1997 to 2019. Not every meadow was surveyed in every year. The trend of decrease ($R^2 = -0.25$) is significant ($p < 0.001$).

as may source populations, reducing overall population stability (Donovan et al. 1996, Loffland et al. 2014). These potentially interacting stressors make restoration and efforts designed to support the region's remaining breeding populations and their habitat more important than ever.

With the exception of one meadow (Stampede) where territory numbers increased during the study (possibly because of a pulse of willow and cottonwood recruitment on a delta of sediment deposited by floods in 1997), the 11 meadows we studied have lost territories since the late 1990s. Most alarming are two meadows (Lacey Valley and Carpenter Valley) that supported a substantial proportion of the local population (6 to 15 territories annually) at the beginning of the study period but where the Willow Flycatcher has often been absent in recent years. In contrast, the two meadows restored a decade ago (Upper and Middle Perazzo) supported similar numbers in the 1990s but their subsequent declines in territory numbers and territory density have been less severe. In fact, since restoration, territory density at these two meadows has been relatively stable in most years, with most of the pre-restoration territory locations remaining occupied over a time long enough to suggest turnover in the individuals occupying the territories. Additionally, flycatchers have colonized some areas of improved habitat in the rewetted

Table 3 Least-Square Means and Confidence Limits for Categories of Restoration in a General Linear Mixed Model Assessing Effects of Pond-and-Plug Meadow Restoration on Density of Willow Flycatcher Territories

Category	Mean	SE	df	Lower CL	Upper CL
Unrestored: After	0.0431	0.0244	10.04	–0.0112	0.0974
Unrestored: Before	0.1207	0.0239	9.26	0.0669	0.1745
Restored: After	0.0739	0.0512	9.64	–0.0406	0.1885
Restored: Before	0.0966	0.0504	9.06	–0.0172	0.2104

Table 4 Pairwise Comparisons of Categories of Restoration in a General Linear Mixed Model Assessing Effects of Pond-and-Plug Meadow Restoration on Density of Willow Flycatcher Territories

Contrast	Estimate	SE	df	*t* ratio	*p*
Restored: After–Restored: Before	-0.0274	0.01552	141.58	−1.764	0.2949
Restored: After–Unrestored: After	0.0261	0.05662	9.72	0.462	0.9657
Restored: After–Unrestored: Before	-0.0514	0.05641	9.57	−0.912	0.7992
Restored: Before–Unrestored: After	0.0535	0.05591	9.24	0.957	0.7759
Restored: Before–Unrestored: Before	-0.0241	0.05569	9.1	−0.432	0.9714
Unrestored: After–Unrestored: Before	-0.0776	0.00846	29.05	−9.17	<0.0001

portions of the restored meadows. Without individually marked birds we cannot know whether these territorial birds hatched at those meadows or immigrated from nearby meadows, but at a minimum we can be confident that the short-term disturbance that pond-and-plug restoration entails did not result in mass emigration away from the restored meadows, as territory numbers at the restored sites did not dip after restoration.

At the regional scale, combining results from the seven meadows with the most consistent data revealed a significant overall decline in territory density of approximately −6% per year. This rate of loss aligns closely with the rate documented at these meadows before the restoration (Mathewson et al. 2013) and with declines in the southwestern subspecies of the Willow Flycatcher (*E. t. extimus*) in southern California (Beatty 2014).

Currently, all Willow Flycatchers in California occur in small, isolated habitat

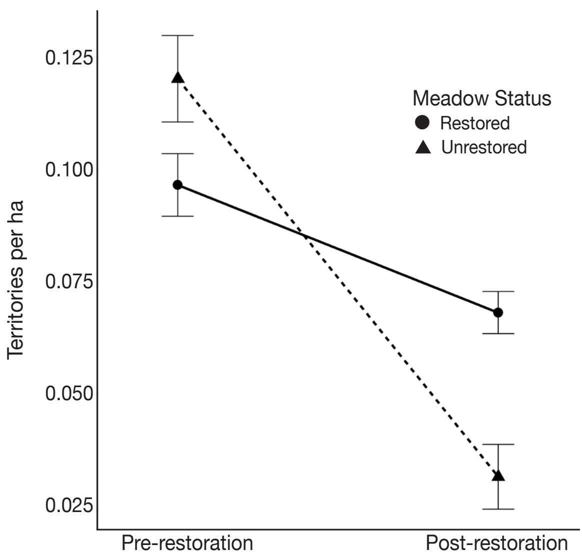

Figure 5. Combined density of Willow Flycatcher territories at the two restored meadows (●) versus at the nine unrestored meadows (▲), before and after restoration was implemented. Error bars indicate the standard error of observed territory density.

patches that support a small number of birds. Populations this small may suffer effects such as the loss of genetic variability, inbreeding depression, or skewed sex ratios (Lacy 1987, Paxton et al. 2002, Kus et al. 2017). At our study sites, before the restoration Mathewson et al. (2013) noted an apparently skewed sex ratio with the number of females declining at a rate greater than that of males. Although we were unable to continue intensive territory monitoring every year after the restoration, we have continued to document many unpaired males (Loffland unpubl. data), suggesting that this skewed sex ratio continues to reduce the population's potential reproductive output. Moreover, a lack of females could mean that results from broadcast surveys, which detect mainly males, may mask population declines that are even more severe than they appear.

Despite the overall decline in territory numbers and density, we also detected a positive effect of restoration. After restoration, territory densities at Upper and Middle Perazzo were essentially stable, even after a precipitous pre-restoration decline at Middle Perazzo, and even as declines continued unabated at most other meadows in the region. In these instances restoration appears to have arrested declines but has not been sufficient to reverse them. The birds' failure to increase during the decade following these meadows' restoration suggests that any benefits of restoration to Willow Flycatcher productivity or survival are not outpacing losses at other stages of this migratory species' annual cycle (Ralph and Hollinger 2003, Paxton et al. 2017). Nonetheless, restoration clearly benefited Willow Flycatchers at the two restored meadows, suggesting that increasing the pace and scale of restoration at as many nearby meadows as possible is worth the effort. Such restoration is being planned for at least two of the larger meadows in our study (Lacey Valley, Carpenter Valley) that harbored multiple territories in the early 2000s and shared many vegetative and physical characteristics with the restored meadows. Their incised channels, lowered water tables, and senescing willow stands could likely be remedied by similar restoration efforts (Balance Hydrologics et al. 2013). Since 2019, two more meadows in our study area, Lower Perazzo and an area downstream from Martis Valley, have also been restored.

Throughout the study area—in restored and unrestored meadows—Willow Flycatchers continue to cluster their territories in the wetter meadows (Sanders and Flett 1989; Loffland unpubl. data) and in areas of those meadows with dense cover of riparian shrubs and ample water (Bombay et al. 2003b). Indeed, Dietrich (2020) found that at Upper Perazzo, Middle Perazzo, and Lacey Valley Willow Flycatchers almost exclusively used areas with >88% soil saturation and >60% sedge cover within the herbaceous layer. Total insect abundance and the abundance of the insect taxa observed being fed to fledglings were also significantly higher in the areas with more saturated soil, indicating that restoration may improve habitat for Willow Flycatcher foraging as well as nesting (ibid.). This affinity for surface water and dense riparian shrubs is consistent with past findings and further emphasizes the importance of meadow moisture and vegetation in maintaining populations (Sanders and Flett 1989, Sedgwick 2000, Bombay et al. 2003b, Green et al. 2003, Vormwald et al. 2011, Dietrich 2020). It should also inform management, as the frequency and intensity of drought in California are projected to increase (Diffenbaugh et al. 2015). Habitat-restoration efforts designed to improve meadow hydrology at Upper and Middle Perazzo appear to have buffered the worst effects of drought during the past decade and likely will continue to do so. In the restored portions of Upper and Middle Perazzo meadows, groundwater remained within 0.6 m of the ground surface from June through August during several drought years (2012–2015). In contrast, at the unrestored Lower Perazzo, groundwater levels fell to 0.9–2.0 m below the ground surface during the dry year of 2015, when shallow monitoring wells were installed at this site (Trustman et al. 2017).

At many meadows, hydrologic restoration by the pond-and-plug and other similar techniques (complete fill, beaver-dam analogs, etc.) may be essential for arresting and possibly reversing the Willow Flycatcher's decline, but where willows and other riparian shrubs have been greatly reduced, we caution that such efforts alone may not be sufficient. In montane meadows, the abundance of meadow-associated bird species is influenced strongly by the structural complexity of the vegetation, particularly the presence of large patches of deciduous riparian shrubs (Campos et al. 2020). With its affinity for willows, the Willow Flycatcher is unlikely to be an exception. In meadows of the northern Sierra Nevada, including some of these same study sites, the response of the Yellow Warbler (*Setophaga petechia*) to restoration was strongest where willow cover was greatest prior to hydrologic restoration (ibid.). In the foothills west of our study, Dybala et al. (2018) also found that the abundance of the Yellow Warbler, Song Sparrow (*Melospiza melodia*), and Warbling Vireo (*Vireo gilvus*), species with similar habitat associations, increased over time as woody vegetation in restored riparian areas increased during the same period as our study. Therefore, in addition to hydrologic restoration, habitat restoration that increases the extent of willow and other deciduous riparian shrubs through targeted management of grazing, planting, and other means should give the Willow Flycatcher the best chance of persisting across the region.

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