ATYPICAL WILLOW FLYCATCHER NESTING SITES IN A RECOVERING RIPARIAN CORRIDOR AT MONO LAKE, CALIFORNIA

CHRIS McCREEDY and SACHA K. HEATH, PRBO Conservation Science, 4990 Shoreline Hwy., Stinson Beach, California 94970

ABSTRACT: Surveys in the 1990s did not find the Willow Flycatcher along Rush Creek, a tributary of Mono Lake, Mono County, California. In 2001 and 2002 we located nine Willow Flycatcher nests along lower Rush Creek, in a riparian corridor currently in its 15th year of long-term rehabilitation after decades of livestock grazing and water diversion for municipal, hydroelectric, and irrigational use. The mated pairs' habitat differs from that reported for the Willow Flycatcher elsewhere in California. Males selected territories in tall thickets of Woods' Rose (Rosa woodsii), and Woods' Rose was the substrate of all nine nests. In addition, the flycatchers' territories and nests were located farther from water than reported elsewhere in California, averaging 129 m for nine nests and 86 m for seven territories.

The Willow Flycatcher (*Empidonax traillii*) is designated as endangered by the California Department of Fish and Game. Estimates of the California population range up to at least 500 territories (Sogge et al. 2003, Green et al. 2003, Craig and Williams 1998, Klamath Bird Observatory unpubl. data, Redwood Sciences Laboratory unpubl. data). Three subspecies of the Willow Flycatcher breed in California (*E. t. adastus, E. t. brewsteri,* and *E. t. extimus*; Unitt 1987). While all three are listed as endangered by the California Department of Fish and Game, *E. t. extimus* is also listed as endangered by the U.S. Fish and Wildlife Service.

Researchers and managers lack taxonomic, habitat, and demographic data for the Willow Flycatcher on the eastern slope of the Sierra Nevada (Craig and Williams 1998), in large part because many of the region's historic populations no longer exist (Gaines 1992, Heath and Ballard 2003). In 2000, we discovered territorial Willow Flycatchers along lower Rush Creek. Situated at Mono Lake, in the heart of the eastern slope, this population represents a likely reoccupation of a riparian corridor that is recovering after decades of water diversion and grazing. The corridor's current rehabilitation has been facilitated by a return of a near-natural streamflow, improved flow management, and a moratorium on grazing that has been in place since 1991 (LADWP 1996). Much effort in California and throughout the West has been directed into modeling potential Willow Flycatcher habitat (Green et al. 2003, C. Stermer pers. comm.). The unique habitat selection of the resurgent population along lower Rush Creek represents an instructive addition to these efforts.

STUDY AREA

Rush Creek is a perennial stream flowing into Mono Lake, California, located at 37.93° N, 119.06° W. It is Mono Lake's largest tributary, with the capacity to carry 75,000 acre-feet of water per year (Gaines 1989). Our study is located on a reach locally known as "lower Rush Creek" (Figure 1),

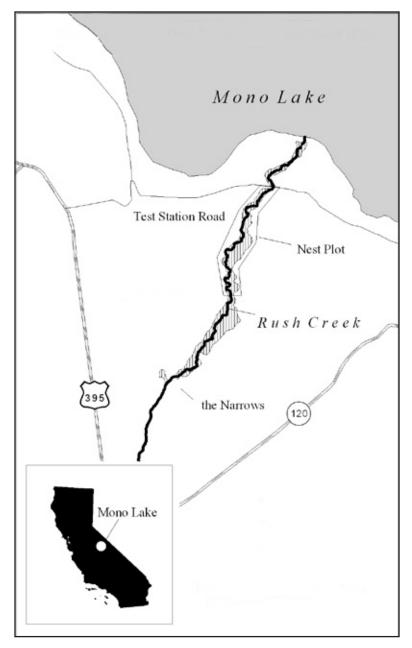


Figure 1. Lower Rush Creek and project study area.

which stretches from a cataract named "the Narrows" (2011 m above sea level) to the Rush Creek–Mono Lake delta roughly 6 km downstream (currently 1945 m above sea level; Stine 1992). This entire section of Rush Creek lies within the Mono Basin National Forest Scenic Area, which is administered by the Inyo National Forest.

Historic Conditions

Lower Rush Creek is recovering after decades of water diversion, altered flood cycles, channelization, and overgrazing (SWRCB 1994). Water diversions for local irrigation and generation of hydroelectric power began in the early 1900s, and diversions to the city of Los Angeles began in 1941 (SWRCB 1994, Stine et al. 1984). Prior to the 1941 diversions, lower Rush Creek was characterized by wide, dense riparian woodland interspersed with wet meadows, standing water, and springs. Pure or mixed stands of willow trees (Salix spp.) and Black Cottonwood (Populus trichocarpa) were interspersed with the less common Jeffrey Pine (Pinus jeffreyi). Descriptions of the understory from this period are scarce, but plant species listed include Woods' Rose (Rosa woodsii), Buffaloberry (Shepherdia argentea), sedges (Carex spp.), rushes (Juncus spp.), grasses, Big Sagebrush (Artemisia tridentata), Bitterbrush (Purshia tridentata), and Rabbitbrush (Chrysothamnus nauseosus) (LADWP 1996, Stine1991).

Grazing of cattle and sheep along lower Rush Creek began in the 1860s and was particularly intense prior to the 1934 Taylor Grazing Act (Jones and Stokes 1993). It is difficult to quantify the extent to which this grazing affected lower Rush Creek's riparian vegetation. Expert testimonies to California's State Water Resources Control Board (1994) suggested that historic grazing pressure on Mono Lake's tributaries caused significant changes to understory plants but that overstory canopies remained largely intact. Additionally, in spite of localized disruptions of stream banks, there were no widespread changes in the stream channel's structure before the 1941 water diversions (SWRCB 1994).

After 1941, water diversions to Los Angeles affected lower Rush Creek's streamflow and, subsequently, its riparian vegetation. From 1941 to 1991, streamflow averaged 52% of the pre-1941 flow. These diversions rendered lower Rush Creek's flow unreliable, and annual streamflow ranged from nine years of none to 173% of pre-1941 flow (the later from flood releases; Los Angeles Department of Water and Power unpubl. data). Lower Rush Creek's high water table was sufficient to support dense vegetation through the 1950s and mid-1960s. Starting in 1967, however, abrupt releases of water from the dam upstream (combined with Mono Lake's concurrent drop in elevation due to diversions) incised and channelized the streambed, lowering the water table and desiccating lower Rush Creek's riparian vegetation (Stine 1992).

Current Conditions

Consistent streamflow returned to lower Rush Creek after the heavy snow of 1989 and a subsequent 1994 state ruling and policy change that curtailed

Los Angeles's water diversions (SWRCB 1994). Lower Rush Creek is currently in the midst of long-term restoration (SWRCB 1998), and from July 2000 through June 2001, lower Rush Creek received 84% of its natural flow (Mono Lake Committee unpubl. data). In addition, the Los Angeles Department of Water and Power has sought to improve its water management by scheduling releases of water to mimic the timing of peak flow in late May and early June, facilitating recharge of the floodplain's water table, improving seed dispersal, and increasing sediment deposition (B. Tillemans pers. comm.). While some streambed restoration and planting have been undertaken since 1995, the riparian corridor's recovery has relied primarily on improved flow management, exclusion of grazing, and natural generation (Ridenhour 1997, J. Bair pers comm.).

In 1991, the Los Angeles Department of Water and Power placed a moratorium on grazing of its lands within the Rush Creek riparian corridor, to increase the likelihood of success of the revegetation (Jones and Stokes 1993). The State Water Resources Control Board (1998) extended this moratorium through 2008, to ensure recovery of riparian and fish habitat. Simultaneously, the Inyo National Forest has phased out grazing on its lower Rush Creek lands, in accordance with the Mono Basin National Forest Scenic Area Management Plan (USFS 1989). Consequently, by 2004 the lower Rush Creek riparian corridor had not been grazed for over 10 years, and its water had flowed continuously for 15 years.

The proportion of riparian to nonriparian cover in lower Rush Creek's riparian zone increased markedly from 1987 to 1999, after restoration of streamflow and release from grazing pressure (McBain and Trush 2003, Kauffman et al. 2000). The riparian zone is currently vegetated with the same plant species observed prior to 1941 diversions, but the structure and composition we see today is early-successional, primarily a mosaic of shrubby stands of mixed willow and Woods' Rose, interspersed with wet and dry meadows and sparse Jeffrey Pine saplings. Black Cottonwoods are less common today than as earlier described (McBain and Trush 2003).

METHODS

Point Counts

As part of more extensive songbird monitoring (Heath and Ballard 2003), we conducted 5-minute, 50-m fixed-radius point counts of all species at 15 stations, spaced 250 m apart and running parallel to the stream, along lower Rush Creek (Figure 2). We followed standards recommended by Ralph et al. (1993 and 1995) and conducted counts three times during the peak songbird breeding season (1 June–4 July) 1998–2000 and two times 2001–2002, spacing each of three or two visits at least seven days apart.

Nest Searching and Territory Mapping

We searched for nests and mapped territories within a 39-ha plot along Rush Creek every one to four days from 5 May to 15 August, 2000–2002 (Figure 2). We located and checked nests on each visit, following the guidelines of Martin and Geupel (1993) and Ralph et al. (1993). Territory sizes

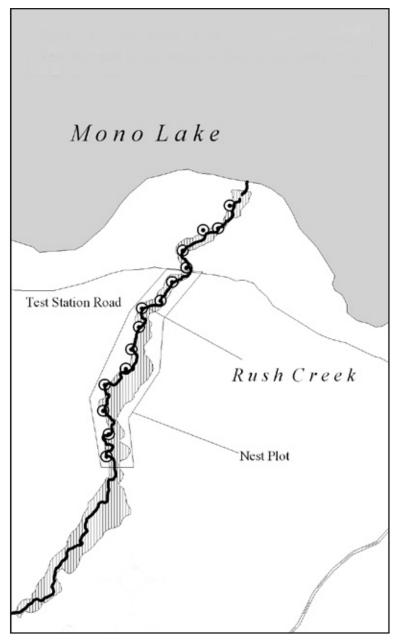


Figure 2. Lower Rush Creek: nest plot and point counts within larger study area.

were estimated from accrued plotted locations of territorial males, as recommended by the IBCC (1970). We assessed vegetation within plots of radii of 5 and 11.3 m around each nest, as described by Martin et al. (1997). We also visually estimated the proportion of major cover types within each plotted territory.

We conducted an additional survey of lower Rush Creek on 15 June 2002, covering the remainder of the riparian corridor for 2.5 km upstream of the nest plot to the Narrows, with the objective of locating and mapping additional Willow Flycatcher territories and finding nests (Figure 1). We continued to map the territory of a mated pair detected on the 15 June survey, monitored this pair's nests once every four days through 10 July 2002, and assessed the vegetation in this territory as described above.

RESULTS

Territories, Nest Establishment, and Phenology

Table 1 summarizes total adult individual Willow Flycatchers observed on lower Rush Creek by year. Two unmated territorial male Willow Flycatchers were observed on lower Rush Creek in 2000. Both sang on territory from 12 June through 30 June, and one defended the same territory until at least 2 August, our last day of surveys. We did not observe a female with either male.

In 2001, lower Rush Creek supported at least four Willow Flycatcher territories. Females and nests were found on three of these territories. Males were first detected on 23 May, and nesting commenced in mid-June (Table 2). The nest plot held a third male (unmated) that sang on territory into early August. On 18 June, during a survey using taped recordings (methods described by Bombay et al. 2000), Inyo National Forest biologists located three birds: a pair, with the male singing, and an apparently unmated male 2 km upstream of the nest plot. We located a nest on the pair's territory at the request of the Inyo National Forest. However, as Inyo National Forest biologists did not find a female with the season's fifth male (Table 1), we did not confirm this fifth territory through subsequent revisits.

In 2002, lower Rush Creek held seven to eight territorial males. Four females nested on these territories, with two females possibly sharing one polygynous male. Nests 5 and 6 were located within 10 m of the successful nests found in 2001. The sole successful nest in 2002 held a buried Brownheaded Cowbird egg.

Table 1 Numbers of Willow Flycatchers along Lower Rush Creek/on Nest-Study Plot, ^a 2000–2002

Year	Adult males	Adult females	Fledged young
2000	2/2	0	0
2001	5/3	3/2	7/7
2002	7-8/2-3	4/3	3/3

^aSee Figure 1.

Table 2 Willow Flycatcher Nesting Phenology along Lower Rush Creek, 2001–02

Nest	Date found	First egg	Clutch size	Cowbird eggs	Hatching date	Fledging date	Nest outcome
2001							
1	18 June	16 June	4	0	1 July	16 July	Fledged 3 young
2	22 June	19 June ^a	4	0	4 July	18 July	Fledged 4 young
3	11 July	Unknown	Unknown	Unknown	Unknown	Unknown	Likely depredated
2002							
4A	15 June	20 June	3	0	_	_	3 eggs depredated
$4B^b$	6 July	Unknown	3	0	_	_	3 eggs depredated
5	21 June	18 June ^a	3	1 buried	3 July	18 July	Fledged 3 young
6	21 June	18 June	4	1	_	_ `	Fledged cowbird
7A	3 July	_	0	0	_	_	Abandoned
$7B^b$	10 July	_	0	0	_	_	Abandoned

^aNest found after clutch completion; date of first egg estimated from date of hatching (Sedgwick 2000).

Five of the territorial males detected in 2002 were upstream of the nest-study plot on 15 June. One was mated; we believed the other four were unmated. Each of the four unmated males remained singing on its territory through 10 July 2002.

Nesting Habitat

Each nest (n=9) was constructed in Woods' Rose. Nest heights averaged 137 cm plus or minus a standard deviation of 7 cm (range 108-160 cm). Woods' Rose, Narrowleaf Willow ($Salix\ exigua$), and Yellow Willow ($S.\ lutea$) provided nest cover. The height of adjacent willow cover averaged $454\pm a$ standard deviation of 36 cm (range 300-600 cm). Nests were constructed in slanted forks off the main stem, and nearby branches of the substrate or an adjacent rose were wound into the nest structure for added support. Although Woods' Rose reached heights of over $3\ m$ in each of the breeding pairs' territories, the average height of shrubs supporting nests was 184 ± 11 cm (range 135-250 cm). Nests averaged $129\pm 18\ m$ from surface water in Rush Creek (range $50-175\ m$). No other surface water was present within this distance at any time during the nesting season.

Breeding-Territory Habitat

Six mated males' territories (three in 2001, three in 2002) averaged 0.78 \pm 0.14 ha in area (range 0.38–1.31 ha). We present results for only six territories because we did not systematically map territories of unmated males outside the study plot and because two of the seven total detected females may have shared one polygynous male. Monotypic stands of Woods' Rose 10–80 m wide dominated five of the six territories. Within the territories, Woods' Rose averaged 63 \pm 9% of vegetation cover (range 20–75%), while willow [Narrowleaf, Yellow, and Shiny (S. lucida)] averaged 25 \pm 2% (range 20–35%). Small pockets of grasses (Leymus triticoides, Elymus elymoides

^bSecond nesting attempt within territory.

ssp. elymoides), sedges (Carex douglasii, C. lanuginosa) and rushes (Juncus mexicanus) generally <10 m across constituted the remaining vegetative cover. Males often used scattered large willows and Buffaloberry snags, which stood over the rose thickets, as song perches. Most of the breeding territories were over 90 m from the closest surface water (the stream itself), and no other surface water was within a territory at any point during the breeding season. The territories' average distance to water was 85 ± 26 m (range 0–150 m). In contrast, all but one of the breeding territories were within 20 m of the riparian corridor's upland sagebrush edge (average distance 11 \pm 5 m, range 0–30 m).

DISCUSSION

The Willow Flycatcher was once a common breeding bird in the Mono Basin (Grinnell and Storer 1924). The collection of the Western Foundation of Vertebrate Zoology (WFVZ) contains multiple pre-1941 nest records for the area, and Joseph Grinnell and James Dixon collected and observed Willow Flycatchers on trips to Mono Lake in mid-June of 1916 and 1937, after most migrants had passed through the region (unpublished records at WFVZ; Grinnell and Dixon field notes at the Museum of Vertebrate Zoology: Unitt 1987). Further information on breeding Willow Flycatchers in the Mono Basin is sparse, with only a few recorded observations of breeding behavior after 1940, none of which were along Rush Creek (Gaines 1992). From May through August 1991, Jones and Stokes (1993: appendixes D and E) conducted extensive bird surveys along lower Rush Creek and detected no Willow Flycatchers. A small population located on the Owens River west of Bishop, Inyo County (75 km southeast of Mono Lake), represents the closest recently confirmed breeding on the Sierra Nevada's eastern slope (M. Whitfield pers. comm.).

Sierra Nevada populations of the Willow Flycatcher, in general, have decreased drastically over the last 50–60 years (Craig and Williams 1998, Serena 1982). Several authors have pointed out that habitat loss, water diversions, and grazing on breeding grounds affect Willow Flycatcher productivity adversely, contributing to population declines in the western United States (Sedqwick 2000, Craig and Williams 1998, Gaines 1992, Serena 1982).

Over the decades of water diversions and grazing, it is difficult to assess habitat conditions on lower Rush Creek quantitatively, for vegetation sampling in the riparian zone has been undertaken only since rehabilitation's onset. However, it is agreed that the lower Rush Creek riparian zone carries significantly more riparian vegetation today than in 1987, at the beginning of restoration (Kauffman et al. 2000, McBain and Trush 2003). Using 1929 photographs of lower Rush Creek as the basis for a pre-1941 baseline of 262 acres of riparian vegetation, McBain and Trush (2003:83) reported a loss of 132.6 acres of riparian vegetation from 1941 to 1989, and a gain of 37.5 acres from 1989 to 1999. Kauffman et al. (2000:254) stressed that, "while the re-watering of the creek is essential for this recovery, it is likely that the cessation of livestock grazing also greatly contributed to the successful establishment and growth of the riparian-obligate species, particularly the willows."

Along lower Rush Creek, territorial male Willow Flycatchers sing frequently and vociferously throughout the mornings, less often in the afternoons (McCreedy pers. obs.). Advertising song is much more common before nest initiation, though unmated males especially may sing through August (Bombay et al. 2000, Sedgwick 2000). There are, however, no recent reports of territorial Willow Flycatchers along Rush Creek prior to our detections of them in 2000 (Heath et al. 2001, Gaines 1992). Willow Flycatchers were reported as absent along lower Rush Creek in 1985 (Jones and Stokes 1993: appendix E), and surveyors did not detect them there near the beginning of rehabilitation in 1991 (Jones and Stokes 1993: appendix E).

The absence of Willow Flycatchers during the 1991 bird surveys along lower Rush Creek, the riparian corridor's easy accessibility, and the dramatic increase in riparian vegetation spurred by the restoration of streamflow and the moratorium on grazing suggest that Willow Flycatchers were absent when restoration began and reoccupied lower Rush Creek some time during the past decade.

Distances to water of the lower Rush Creek nest sites and territories differ from those reported elsewhere in California. In a summary of California Willow Flycatcher data, Craig and Williams (1998) reported that water is always present in territories of *E. t. brewsteri*, while nests of *E. t. extimus* nests average a distance of 21 m to water. In the northern and central Sierra Nevada King and King (2003) found open water to cover 4% of ground cover within 5 m of 10 Willow Flycatcher nests, and Bombay et al. (2003) found standing water or saturated soils to cover an average 44% of 87 territories. In addition, King and King (2003) reported complete soil saturation at all nest sites.

For nine nests and six territories along lower Rush Creek (2001–2002), the average distance from a nest to surface water was 129 m, and the average distance from a territory to water was 86 m. Although our study did not assess soil saturation directly, distances of nests and territories to saturated soil along lower Rush Creek would be shorter than distances to surface water. Through our study, however, stream flows in the study area were tightly regulated by releases from water impoundments upstream. Past channelization of Rush Creek and below-average peak flows kept surface water confined to the streambed even during nest-site selection, which coincides with Rush Creek's yearly peak flow. Although low-lying pockets of saturated soil exist away from the streambed, they are often small and isolated, particularly around several of the flycatcher territories (McCreedy pers. obs.). In addition, in a ranking of Rush Creek's and nearby Lee Vining Creek's 13 riparian plant communities, McBain and Trush (2003:42) put the "Narrowleaf Willow-Rose" and "Rose" patch types (which contain the Willow Flycatcher territories on lower Rush Creek) in eight and ninth place, respectively, closer to the dry end of the spectrum. Across the lower Rush Creek corridor, where soil is more saturated, Woods' Rose gives way in understory dominance to young willows.

In the six territories along lower Rush Creek (2001–2002), the average cover of willow was 24%, and the average cover of rose was 64%. All nine nests were in Woods' Rose. In contrast, in an unpublished 1997 U. S. Forest Service protocol for surveying for Willow Flycatchers, J. H. Harris described

Willow Flycatcher habitat in the central and southern Sierra Nevada as "willow-dominated," with "moist meadows with perennial streams and smaller spring-fed or boggy areas with willow or alder." More recently in the Sierra Nevada, Bombay et al. (2003) linked nest and territory selection to riparian shrub cover (98% of riparian shrub cover was willow at the territory scale, and 99% was willow at the nest scale). King and King (2003) found 10 of 10 nests built in Mountain Alder (Alnus incana), and nine of these nests were completely surrounded by Lemmon's Willow (Salix lemmonii). In addition, the U. S. Forest Service's current survey protocol for the Willow Flycatcher does not include dry, monotypic stands of rose among its five general types of Willow Flycatcher habitat in central and northern California (Bombay et al. 2000:26–27).

The habitat along lower Rush Creek may most closely recall King's (1955) report on a wide range of nest substrates for Willow Flycatchers in the Palouse Hills of southeastern Washington, encompassing a spectrum of mesic to xeric habitats. Thirty-six percent of the Palouse Hills nests were built in Rosa spp., in what King referred to as "upland prairie remnants." The Palouse Hills nests averaged a distance of 37 m to standing water. Though we are reluctant to label the riparian Rush Creek rose fields as "xeric" (as did King for his upland habitats), the average distance from nests to water along lower Rush Creek is over three times that in the Palouse Hills.

The dynamics that created this anomalous breeding habitat are worth further discussion. Starting in 1941, diversions of four of Mono Lake's tributaries dropped the lake's level 45 feet by 1982 (Ridenhour 1997). As the lake's level fell, Rush Creek's gradient sharpened. Cutting and deepening of the creek's channel resulted, compounded by releases of large volumes of water during years of heavy snow (Stine 1991). Lower Rush Creek's historic riparian vegetation became isolated on terraces above the riparian corridor's descending groundwater table, and it was no longer subject to flooding during years of heavy runoff. At least 80% of lower Rush Creek's collapsed riparian forest died. Woods' Rose and Narrowleaf Willow survived best on these terraces, outcompeting drought-intolerant riparian obligates. Often, the rose and willow on these terraces stood over 100 m from the current streambed. Recent restoration of consistent streamflow through lower Rush Creek has recharged the riparian corridor, halting the terraces' slow change to sagebrush scrub, and the surviving Woods' Rose and Narrowleaf Willow were in the best position to recolonize and dominate the recharged riparian corridor (J. Bair and B. Tillemans pers. comm.).

Aerial photographs of Rush Creek taken in 1929, before diversion of water to Los Angeles, show large patches of Woods' Rose, though in locations different from today's (McBain and Trush 2003:37). Contemporary passive restoration of lower Rush Creek has resuscitated this component of the riparian habitat, which is now used by an increasing population of Willow Flycatchers. In addition, groundwater recharge is sufficient to support small stands of the riparian-obligate Yellow and Shiny Willows within each Willow Flycatcher territory; these taller trees are important for song and foraging perches (McCreedy pers. obs.). Additional unoccupied areas of this rose—willow mix exist along lower Rush Creek, across the Mono Lake

Basin, and at lower elevations throughout the eastern Sierra Nevada. If the Willow Flycatcher's productivity and survivorship along lower Rush Creek remain high, this population may provide a source for the reoccupation of other riparian areas in the region. Continued monitoring of its productivity, site fidelity, and territory and nest-site selection will instruct us on this species' likely reoccupation and population expansion on recovering lower Rush Creek.

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