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ABSTRACT: The Willow Flycatcher has been declining throughout the Sierra Nevada and within Yosemite National Park since at least the middle of the 20th century. More recently, the number of Willow Flycatchers captured at a bird-banding station in Yosemite declined during the 1990s, with none captured since 2002. We used historical records and digital maps based on remote sensing to identify and survey Yosemite's most likely breeding habitat for the species. Over the 2006 and 2007 breeding seasons we visited 71 sites, which accommodated 1709 call stations. We detected no territorial Willow Flycatchers, and we conclude that the species no longer breeds in Yosemite National Park. The extirpation of this species from Yosemite, where so much protected, apparently high-quality habitat remains, suggests that causes in addition to direct effects of recent land-management practices have contributed substantially to the decline of the species across the Sierra Nevada.

The Willow Flycatcher (*Empidonax traillii*) has declined precipitously in the Sierra Nevada since the middle of the 20th century (Harris et al. 1987, Stefani et al. 2001, Green et al. 2003). Three subspecies of the Willow Flycatcher—*E. t. brewsteri*, *E. t. adastus*, and *E. t. extimus*—occur in the Sierra Nevada, and 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. Early in the 20th century the species was described as "common" in Yosemite Valley (Gaines 1992) and through much of the Sierra Nevada (Grinnell and Miller 1944), but by 2003, Green et al. (2003) were able to tally just 315 Sierran territories known to have been occupied at some time since 1982. Bombay et al. (2001) estimated population growth rates in the range of 0.768 to 0.869 in their Sierran study area, indicating a continuing population decline.

In a comprehensive review of possible causes of Willow Flycatcher decline in the Sierra Nevada, Green et al. (2003) determined that reduced fecundity due to high rates of nest predation, rather than poor survival of adults or recruitment of juveniles, was likely the primary demographic cause. They reviewed return rates of adults and juveniles from multiple Sierra Nevada locations and concluded that adult survival and juvenile recruitment within the Sierra Nevada fell within the range observed for Willow Flycatcher populations in other bioregions. Cain et al. (2003) found that standing water around nests is a deterrent to predation by mammalian predators, and Green et al. (2003) suggested that high rates of nest predation are a result of gradual desiccation of meadows, resulting from livestock trampling, road construction, human recreation, harvesting of adjacent timber, forest thinning for fire control, fire suppression, water diversions, mining, and perhaps climate change.

If meadow desiccation resulting primarily from land-management pressures is indeed the driving cause of Willow Flycatcher decline in the Sierra Nevada, we might expect a less pronounced decline in Yosemite National

Park, where the deleterious effects of these activities, since at least the middle of the 20th century, have presumably been less severe than elsewhere in the Sierra Nevada. Yet the species has clearly declined in Yosemite as well. Although detailed historical information about the species' distribution and abundance in the park is lacking, Willow Flycatchers nested commonly in Yosemite Valley at least into the early 20th century (Grinnell and Storer 1924) and were "vocal, conspicuous birds" in suitable habitat throughout the lower elevations of the park until at least the 1930s (Gaines 1992). But the species has not nested in Yosemite Valley since 1966 (Gaines 1992), and in the late 1980s Gaines (1992) estimated there were fewer than 30 pairs remaining in the greater Yosemite area.

Further evidence suggests declines in Yosemite's population have continued. Yosemite has hosted five bird-banding stations associated with the Monitoring Avian Productivity and Survivorship (MAPS) program (DeSante and Kaschube 2006, DeSante et al. 2007) since the early 1990s. The MAPS station at Hodgdon Meadow captured Willow Flycatchers every year between 1991 and 1997, but the number of captures declined through the 1990s, and no Willow Flycatchers have been captured at the station since 2002 (Figure 1). Evidence suggests that many of the birds caught at Hodgdon Meadow were not just migrating or dispersing birds but summer residents at the station, at least during the first half of the 1990s. During that time nine individuals were caught in two or more years, and seven of those birds were caught after 15 June in at least one year. Before 1996 seven birds with

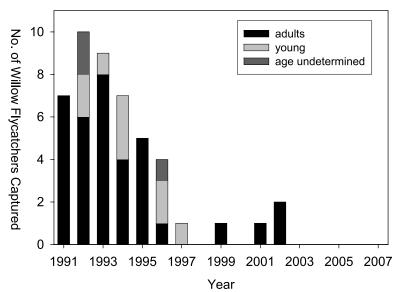


Figure 1. Annual number of Willow Flycatchers mist-netted at the Monitoring Avian Productivity and Survivorship (MAPS) station at Hodgdon Meadow, Yosemite National Park.

well-developed brood patches were captured, but none with brood patches have been captured since then.

Bombay et al. (2000) reviewed the Willow Flycatcher's nesting habitats in the Sierra Nevada. The species nests most typically in willow thickets in or adjacent to low- and mid-elevation meadows or riparian stringers covering at least 0.4 ha, usually considerably more (Figure 2). Nests have also been found in willow thickets adjacent to lakes, marshes, and creeks. Less frequently, Willow Flycatchers have nested in patches of riparian deciduous shrubs other than willows. Nesting areas, at least in the early part of the breeding season, generally are characterized by extensive surface water (Harris et al. 1988. Sanders and Flett 1989, but see also McCreedy and Heath 2004) and substantial openings, either large and continuous or small and numerous, in the forest canopy. The micro-site used for nesting is typically a patch of shrubs 2-4 m tall, with a high density of leaves (Sanders and Flett 1989, Bombay 1999). Historical records from the Yosemite area suggest Willow Flycatchers bred commonly in the park below 1525 m and less frequently at higher elevations (Gaines 1992). The highest recorded breeding pairs in the park were observed at around 2150 m (Gaines 1992), consistent with Bombay's (1999) suggestion that the upper elevation limit of breeding habitat is determined by the presence of snow and leafless willows at the time of spring arrival.



Figure 2. Potential Willow Flycatcher nesting habitat at Ackerson Meadow, just outside Yosemite National Park.

Photo by Bob Wilkerson

METHODS

As a prelude to investigating factors affecting the Willow Flycatcher's reproductive success in Yosemite, we conducted a nearly comprehensive two-year inventory of appropriate habitat throughout the park. Our goal was to locate all remaining Willow Flycatcher territories in Yosemite rather than merely estimate the size of the park's breeding population. We therefore sought to identify and survey all of the park's most promising habitat patches rather than to select a random subsample of the park's patches of potential habitat.

We developed a classification of sites we believed most likely to host breeding flycatchers and prioritized them for surveys according to the following process:

Priority 1 sites: We classified any sites where Willow Flycatchers were detected during the past 30 years as priority 1, regardless of the habitat's characteristics (although all such sites were meadows or riparian areas) or whether birds had been confirmed to be breeding at the site. We collated information on these sites from our own work in the park over the past 18 years, from published and unpublished reports, and by consulting with researchers and knowledgeable birders who have worked extensively in Yosemite over the past decades and/or are experts on Willow Flycatchers in the Sierra Nevada. Priority 1 sites were slated to be surveyed in both years (2006 and 2007) of our two-year study.

Priority 2 sites: We studied Yosemite National Park's digital maps based on remote sensing to identify additional patches of potential habitat not known to have had Willow Flycatchers during the past 30 years. Starting with all patches of willows and other riparian shrubs indicated on the park's most recent vegetation map (completed in 2003), we discarded from consideration all patches at elevations greater than 2440 m (see Gaines 1992). We grouped the remaining 454 patches into clusters of nearby patches that were generally within 500 m of one another, though typically even closer, and were part of the same riparian system. Clusters of habitat patches that contained at least 1.0 ha (combined) of willows or other riparian deciduous shrubs, were interspersed with substantial openings in the forest canopy, and appeared to have a nearby source of surface water, we classified as priority 2, for survey in either 2006 or 2007.

Priority 3 sites: We classified sites that met all the above requirements except for interspersion with openings in the forest canopy as priority 3, for survey in only one year of our study, if time permitted.

At the beginning of each field season, we provided our crew with a weeklong training session. Before they could conduct surveys, we required all crew members to pass an exam testing their ability to identify by sight and sound Willow Flycatchers and species with which they could be confused.

Our survey methods adhered closely to those developed by Bombay et al. (2000). In brief, the survey protocol requires broadcasting recordings of Willow Flycatcher songs to elicit responses from territorial birds. We visited each site at least twice during the breeding season, once between 15 and 25 June, and once either between 1 and 14 June or between 26 June and 15 July. Surveys began 1 hr before official sunrise or as soon as there was adequate light to see birds and were always completed or suspended by 10:00. Survey points were spaced 30–50 m apart in suitable habitat.

If there was no suitable habitat, no survey points were established. During the second visit to each site, we did not ensure that individual survey points were placed exactly in the same location as in the previous visit, as the park's wilderness regulations prevented us from marking survey points, and relocating exact points without markers proved time-consuming; instead, we simply made sure that the same general areas were resurveyed. As a result we often surveyed a slightly different number of points during the two visits to a site. At each survey point observers first listened quietly for 1 min, then completed two cycles of broadcasting *fitz-bew* vocalizations for 30 seconds followed by listening quietly for 2 min.

RESULTS

Our site-selection process yielded 12 priority 1 sites, 40 priority 2 sites, and 21 priority 3 sites distributed across the lower and middle elevations of the park (Figure 3). During the two-year study, we visited 71 of our 73 selected sites (Appendix 1); two particularly remote priority 2 sites in the northwestern corner of the park proved to be inaccessible because of cliffs and streams that could not be crossed safely. Visits to six of the selected sites revealed no suitable Willow Flycatcher habitat. The spatial extent of the 65 survey sites where we found suitable habitat varied greatly, with individual sites accommodating as few as 3 and as many as 128 call stations (average 27 call stations per site). Sites classified as priority 1 were surveyed in both 2006 and 2007; the remaining sites were surveyed in either 2006 or 2007.

We detected Willow Flycatchers only twice during our surveys, and both detections were of nonterritorial birds at Wawona Meadow. On 1 June 2006, the first day of the field season, two Willow Flycatchers responded to our broadcast survey at the same call station at Wawona Meadow. Both birds repeatedly made the *fitz-bew* vocalization, and one of the birds was also observed at close range for approximately 20 minutes. We could not relocate the birds when we returned to the site the following day and then again later in the season. Because we repeatedly searched the meadow while broadcasting recordings of vocalizations and spent extra time searching the area around the detection, we are certain neither of the birds remained and held a territory at Wawona. In their protocol, Bombay et al. (2000) set the date of survey initiation at 1 June but cautioned that "migrants may still be present and singing during this period." Indeed, in a small population east of Yosemite Willow Flycatchers sometimes do not appear at their breeding sites until the first or second week of June (McCreedy 2006, 2007).

On 4 July 2007, we detected a Willow Flycatcher at Wawona Meadow, though this time the identification could not be 100% certain because the bird did not vocalize. Nevertheless, the observer was an experienced birder who recorded detailed and persuasive notes about the appearance of the bird. The bird had not been detected during two previous surveys of the site in June. After the detection, a return visit to the site the following day failed to relocate the bird, even with the use of playback and intensive searching by multiple observers. Our surveys of Wawona Meadow throughout the breeding season leave us certain the bird did not maintain a breeding territory at the site in either 2006 or 2007.

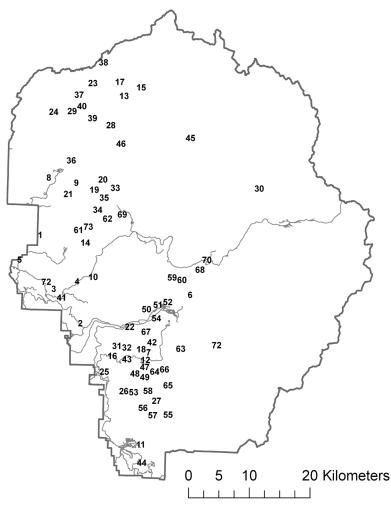


Figure 3. Sites targeted for Willow Flycatcher surveys in Yosemite National Park. Thin gray lines indicate paved roads. Sites 1-12 were priority 1; sites 13-52 were priority 2; sites 53-73 were priority 3. See Appendix 1 for site names and location coordinates.

DISCUSSION

Our failure to detect any territorial Willow Flycatchers strongly suggests that they no longer breed in Yosemite National Park. Although it was not possible to survey every patch of riparian deciduous vegetation in the park, we were able to survey virtually all the patches that seemed, on the basis of

the best available data and published descriptions of habitat characteristics, most likely to host breeding Willow Flycatchers. Sites with detections during the previous 30 years were fully surveyed in both 2006 and 2007.

The detections of apparently nonterritorial birds at Wawona Meadow suggest that even though Willow Flycatchers clearly did not breed at the site during the last two years, the site has been visited by migrants or nonbreeders. Indeed, the meadow may have been occupied by at least one pair of Willow Flycatchers in the last decade, as an adult female with a well-developed brood patch was mist-netted there in 1999 (Wilkerson and Siegel unpubl. data). This evidence is not conclusive, however, as females with brood patches have been captured in the Mono Basin on nest plots where they apparently did not breed (Chris McCreedy pers. comm.). Nevertheless, continued visitation by Willow Flycatchers, even if they apparently spend most of the breeding season elsewhere, suggests that Wawona Meadow merits continued monitoring during the breeding season.

The apparent extirpation of Willow Flycatchers from Yosemite gives perspective on the causes of the species' decline in the rest of the Sierra Nevada. Green et al. (2003) identified anthropogenic meadow desiccation as the primary cause of Willow Flycatcher decline in the Sierra Nevada. Because Willow Flycatcher declines at Yosemite have mirrored declines throughout the Sierra Nevada, it is parsimonious to assume that the causes of decline at Yosemite and elsewhere in the Sierra Nevada are similar. Throughout the 20th century cattle grazing and other types of land management had substantial effects on meadows across the greater Sierra Nevada (Menke et al. 1996), but it seems puzzling that similar, recent declines of the Willow Flycatcher have occurred in the park, where most riparian habitat has been largely free of livestock grazing for many decades (Blaney and Moore 2001). Although we did not quantify vegetation and hydrological conditions at each site rigorously, willows throughout the park during our study generally had dense foliage and appeared healthy. Most sites had some standing water or saturated soils during our survey visits, even in 2007 after a winter with an unusually small snowpack.

The Willow Flycatcher's decline in Yosemite during the first half of the 20th century could have resulted from the dramatic changes in the meadows' plant communities triggered by heavy sheep grazing (Beesley 1996, Dull 1999) between the 1850s and the early 1900s (Farquhar 1976, O'Neill 1983) or the heavy grazing by pack animals that continued in the park well into the 20th century (Blaney and Moore 2001). It seems less plausible that such long-past activities continue to drive more recent declines, although Cooper et al. (2006) suggested that soils and plant communities in at least some Yosemite meadows still have not recovered from sheep grazing that ceased over a century ago.

Another possibility is that Yosemite's meadows are still drying out but in response to climate cycles or climate change rather than to grazing or other land-management practices. Warmer temperatures earlier in the year could reduce standing water later in the summer. Research on meadow hydrology in relation to climate change and climate cycles is warranted, as predictions for the Sierra Nevada include reduced snowpack and earlier, more rapid

spring snowmelt (Gleick et al. 2000). Such changes could have substantial effects on meadow-nesting birds, if they have not already.

Gaines (1992) suggested an alternative hypothesis for the Willow Flycatcher's decline in Yosemite, that suitable habitat within the park is insufficient to sustain a viable population without immigration from neighboring areas. Under this scenario of disrupted metapopulation dynamics, Yosemite's declines could be explained by habitat degradation outside the park, regardless of habitat condition within the park. Yosemite appears to have no shortage of suitable Willow Flycatcher habitat, however. The sites we surveyed accommodated 1709 survey points within apparently suitable habitat. Assuming that each survey point was placed to survey a 20-m radius circle of suitable habitat surrounding it, we visited and surveyed approximately 215 ha of suitable habitat within the park. Published values suggest that Willow Flycatcher territories in the Sierra Nevada generally average less than 0.4 ha (Sanders and Flett 1989, Craig and Williams 1998), implying that the habitat patches we surveyed in the park could theoretically host hundreds of Willow Flycatcher territories, although the birds probably never saturated the available habitat so completely. Some of the habitat patches we judged "suitable" probably were not optimal. For example, some proved to be composed primarily of brown dogwood (Cornus glabrata) or other deciduous riparian shrubs rather than willows. But even if a substantial portion of the sites we surveyed is excluded from consideration. Yosemite may still offer adequate habitat area for a self-sustaining Willow Flycatcher population, depending on metapopulation dynamics. Modeling metapopulation dynamics to assess whether a population sink outside the park could explain population declines within the park, perhaps even in the absence of habitat degradation within the park, could help resolve this question.

Conditions on the wintering grounds or along migration routes, rather than on the Sierra Nevada breeding grounds, could be driving declines, but available information on the survival rates of adult Willow Flycatchers in the Sierra Nevada (Bombay et al. 2001) suggests that survival and/or return rates in the region appear comparable to or higher than those in other regions (Green et al. 2003), including southeastern Oregon (Sedgwick and Klus 1997, Sedgwick and Iko 1999) and the southwestern United States (Stoleson et al. 2000). Other hypotheses that might explain the decline at Yosemite—continuing effects of severe habitat degradation during the 19th century, more recent meadow desiccation due to climate change, and the disruption of metapopulation dynamics due to habitat degradation at sites outside the park—all warrant further study.

Most of the potential causes of the Willow Flycatcher's decline discussed above suggest that improved management of the species' riparian and meadow breeding grounds throughout the Sierra Nevada could aid its recovery. Regardless of whether other factors are also contributing to the decline, good management of breeding habitat is surely a critical component of the species' persistence in the Sierra Nevada. Furthermore, any measures taken to improve or restore montane meadows across the Sierra Nevada will likely benefit the many other bird species that also breed or forage in montane meadows.

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APPENDIX	1	Sites	selected	for	Willow	Flycatcher	surveys	in	Yosemite
National Par	k.								

Site number	Priority ^a	Site name	Latitude (° N)	Longitude (° W)	No. of survey points ^b	Year of last detection
1	1	Ackerson Meadow	37.8331	119.8325	7.3	1999 ^c
2	1	Big Meadow	37.7044	119.7532	26.0	2004 ^d
3	1	Crane Flat	37.7540	119.8043	10.3	2001e
4	1	Gin Flat	37.7663	119.7611	0	2000f
5	1	Hodgdon Meadow	37.7959	119.8700	51.0	2002^{g}
6	1	Mirror Lake	37.7510	119.5498	35.0	2005 ^h
7	1	Peregoy Meadow	37.6644	119.6242	44.5	1974 ⁱ
8	1	Poopenaut Meadow	37.9183	119.8198	11.5	1999j
9	1	Smith Meadow	37.9119	119.7680	7.5	1999^{k}
10	1	Upper Tamarack Creek	37.7734	119.7359	0	1996 ¹
11	1	Wawona Meadow	37.5277	119.6380	128.0	2007^{m}
12	1	Westfall Meadows	37.6528	119.6342	15.3	1986^{n}
13	2	Andrews Lake	38.0421	119.6878	24.0	
14	2	Aspen Valley East	37.8236	119.7524	23.0	
15	2	Avonelle Lake Northwest	38.0554	119.6564	28.5	
16	2	Badger Pass	37.6625	119.6593	25.5	
17	2	Bearup Lake	38.0626	119.6965	10.0	
18	2	Bridalveil Creek II	37.6691	119.6163	13.5	
19	2	Cottonwod Creek East	37.9028	119.7123	37.5	
20	2	Cottonwood Creek Headwaters	37.9177	119.7231	2.5	
21	2	Cottonwood Meadow	37.8947	119.7870	69.0	
22	2	Crocker Point Southwest	37.7011	119.6652	38.5	
23	2	Edith Lake	38.0596	119.7471	7.0	
24	2	Eleanor Creek	38.0156	119.8189	23.5	
25	2	Elevenmile Meadow	37.6338	119.7101	23.5	
26	2	Empire Meadows	37.6066	119.6436	90.5	
27	2	Empire Meadows West	37.6102	119.6119	31.0	
28	2	Falls Creek West Tributary	37.9983	119.7112	34.5	
29	2	Frog Creek Headwaters	38.0180	119.7584	9.0	

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Site	Duinuitad	Cite manual	Latitude	Longitude (° W)	No. of survey	Year of last
number	Priority ^a	Site name	(° N)	(VV)	points ^b	detection
30	0	Glen Aulin	27 0107	119.4305	75	
	2		37.9107		7.5	
31	2	Grouse Creek I	37.6724	119.6838	19.0	
32	2	Grouse Creek II	37.6704	119.6696	14.0	
33	2	Harden Lake Northwest	37.9059	119.6994	17.0	
34	2	Harden Lake Southwest	37.8732	119.7114	19.0	
35	2	Harden Lake West	37.8909	119.7198	13.5	
36	2	Hetch Hetchy	37.9445	119.7831	14.0	
					14.0 0	
37	2	Kendrick Creek	38.0419	119.7721		
38	2	Kendrick Creek Headwaters	38.0907	119.7283		
39	2	Lake Vernon Southwest	38.0078	119.7459	31.0	
40	2	Laurel Lake Headwaters	38.0251	119.7663	25.5	
41	0		27 7414	110 7026	0	
41	2	Little Crane Creek	37.7414	119.7936		
42	2	McGurk Meadow	37.6792	119.6229	28.3	
43	2	Monroe Meadows South	37.6533	119.6686	16.0	
44	2	South Entrance	37.5008	119.6355	62.0	
45	2	Table Lake	37.9827	119.5615	13.5	
46	2	Tiltill Valley	37.9714	119.6910	33.5	
47	2	Westfall Southeast I	37.6428	119.6144	6.0	
	2					
48	2	Westfall Southeast II	37.6331	119.6231	10.5	
49	2	Westfall Southeast III	37.6279	119.6139	9.5	
50	2	Yosemite Valley I	37.7285	119.6083	9.5	
51	2	Yosemite Valley II	37.7351	119.6057	16.0	
52	2	Yosemite Valley III	37.7393	119.5955	23.0	
53	3	Alder Creek	37.6048	119.6544	41.5	
54	3	Cathedral Beach Southeast	37.7148	119.6158	0	
55	3	Chilnwalna Creek	37.5730	119.5893	31.5	
	3					
56		Chilnwalna Falls I North	37.5823	119.6191	3.0	
57	3	Chilnwalna Falls North II	37.5715	119.6176	20.0	
58	3	Empire Meadows Southeast	37.6073	119.6279	26.0	
59	3	Indian Canyon Creek	37.7760	119.5805	0	
60	3	Lehamite Creek	37.7726	119.5702	0	
61	3	Lower Long Gulch Creek	37.8422	119.7578	22.0	
62	3	Middle Fork Tuolumne	37.8601	119.7122	83.0	
63	3	Mono Meadow East	37.6708	119.5689	23.5	

APPENDIX 1 (continued)

(continued)

Site number	Priority ^a	Site name	Latitude (° N)	Longitude (° W)	No. of survey points ^b	Year of last detection
64	3	Ostrander Lake Northwest	37.6367	119.5895	13.0	
65	3	Ostrander Lake West	37.6163	119.5908	25.5	
66	3	Peregoy Southeast	37.6398	119.5982	41.5	
67	3	Pohono Trail	37.6946	119.6344	14.0	
68	3	Porcupine Creek	37.7919	119.5371	21.5	
69	3	Siesta Lake Northwest	37.8668	119.6848	41.0	
70	3	Snow Creek	37.8033	119.5247	23.5	
71	3	Tuolumne Grove	37.7645	119.8082	18.5	
72	3	Upper Illilouette Creek	37.6776	119.5023	35.0	
73	3	Upper Long Gulch Creek	37.8473	119.7476	9.0	

APPENDIX 1 (continued)

^aSee Methods for an explanation of priority rankings.

^bThe number of survey points observers placed in suitable habitat, averaged over all visits to the site. Numbers varied slightly from visit to visit, as observers had discretion to place points 30–50 m apart. Entries of "0" indicate that the site had no suitable habitat.

 $^{\rm c} {\rm One}$ bird heard singing (outside park boundaries) in June by Adam Rich, Stanislaus National Forest.

^dTwo adults captured at MAPS station in early June.

^eOne adult captured at MAPS station in mid-June.

^fOne adult captured at MAPS station in August.

^gTwo adults captured at MAPS station, one in June, one in July.

^hTwo individuals observed by Kurt Mize in late May.

ⁱOne singing bird heard by David DeSante in June.

/Two adults mist-netted in August.

^kOne adult mist-netted in August.

¹One adult captured at MAPS station in August.

 $^m\!Not$ territorial; see text. Last report prior to this study: one female with a well-developed brood patch mist-netted in July 1999.

ⁿOne singing bird heard by Jon Winter in June.

•Not surveyed because cliffs and stream crossings made access too dangerous.

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Willow Flycatcher

Sketch by Zev Labinger