

DIET OF NESTLING WILLOW FLYCATCHERS IN MEADOWS OF THE SIERRA NEVADA

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ABSTRACT: I used video observations to quantify the diet of nestling Willow Flycatchers (*Empidonax traillii*) at six nests in two meadows (Middle Perazzo and Lacey) on the eastern slope of the Sierra Nevada, California. Prey fed to the nestlings consisted primarily of Diptera (24%), Odonata (22%), Ephemeroptera (16%), Lepidoptera (12%), and Raphidioptera (12%). Other less abundant taxa in the diet included Orthoptera, Coleoptera, and Hymenoptera. Aquatic insects such as Ephemeroptera and Odonata were fed more commonly at the five nests at Middle Perazzo Meadow, whereas terrestrial insects such as pollinating Diptera, Hymenoptera, Orthoptera, and Raphidioptera predominated at the single nest observed at Lacey Meadow. At Middle Perazzo Meadow nestlings in nests situated closer to the meadow's edge were fed more Raphidioptera, whereas those in nests farther from the edge were fed more Ephemeroptera and Odonata. Raphidioptera were fed more frequently in the morning and evening, whereas Diptera, Hymenoptera, Lepidoptera, Hemiptera, and Orthoptera were generally more frequently offered in the middle part of the day. Ephemeroptera were most often provided in the afternoon and evening while feedings with Odonata fluctuated little through the day.

Studies of the Willow Flycatcher's diet in the western United States have focused largely on the Southwestern Willow Flycatcher (*Empidonax traillii extimus*), addressing temporal and spatial variation in its diet as well (Drost et al. 2003, Wiesenborn and Heydon 2007, Durst et al. 2008). The foods and food/habitat relationships of other subspecies such as *E. t. brewsteri*, which breeds in the Sierra Nevada and Pacific Northwest, have received little attention. Green et al. (2003) suggested that the Willow Flycatcher's diet is similar across its breeding range, but my study in Sierra meadows suggests otherwise (Dietrich 2020). Preliminary results imply that the Willow Flycatcher's diet may vary by location, habitat, and time of day (Dietrich 2020), but more evidence is needed to support these findings. Here I report observations of food items fed to nestling Willow Flycatcher at six nests in two meadows of the Sierra Nevada.

STUDY AREA

Located on the east slope of the Sierra Nevada in Sierra County, California, the Little Truckee River watershed is home to one of the largest and most persistent populations of the Willow Flycatcher in the Sierra Nevada (Serena 1982, Harris et al. 1987, Sanders and Flett 1989, Green et al. 2003). In the summer of 2021, I monitored six Willow Flycatcher nests in this watershed, five at Middle Perazzo Meadow and one at Lacey Meadow (Figure 1). Lying at an elevation of 1981 m in a broad valley, Middle Perazzo Meadow features large ponds formed by natural river processes and pond-and plug-restoration in 2013 (Loffland et al. 2022). Its vegetation is dominated by shrubby willows (*Salix* spp.) and sedges (*Carex* spp.). At 2134 m elevation Lacey Meadow also occupies a large river valley but lacks the abundance of wetland vegetation

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found in Middle Perazzo Meadow and is covered mostly with grasses and forbs; willows grow only near the main river channel. Both meadows are closely surrounded by forest of Lodgepole Pine (*Pinus contorta*); Middle Perazzo Meadow is also partially bordered by sagebrush (*Artemisia tridentata*).

METHODS

Video Sampling

I used a high-resolution, tripod-mounted video camera (Lumix G85) and telephoto lens (Leica, 100–400 mm) to video-record nests at a distance of 3 to 5 m from the nest with a clear view of nestlings. Each nest was recorded during five periods of the day, early morning (06:00–09:00 PDT), late morning (9:00–12:00), early afternoon (12:00–15:00), late afternoon (15:00–18:00), and evening (18:00–21:00). This was done in order to get a more representative sample of the diet throughout the day and to be able to compare the diet by subsets of the day. Typically, a minimum of 3 to 4 hours of recorded video was needed for each period. Since sufficient video could not be recorded in a single day, I recorded the nests for 2 to 4 successive days. Thus I recorded

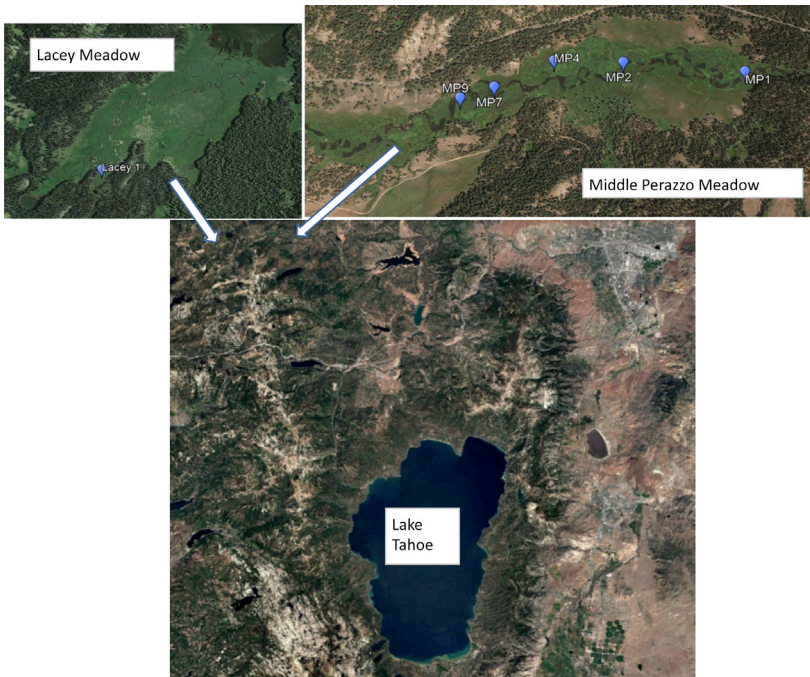


FIGURE 1. Study area, Middle Perazzo and Lacey meadows, Sierra County, California.

Photos from Google Earth

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TABLE 1 Effort Video-Recording and Provisioning of Willow Flycatcher Nestlings in Middle Perazzo and Lacey Meadows, Sierra Nevada

	Lacey	Middle Perazzo ^a				
		MP1	MP2	MP4	MP7	MP9
Dates	25–28 Jul	8–10 Jul	21–23 Jul	14–15 Jul	17–18 Jul	19–20 Jul
Estimated age of young (days)	8–12	4–8	8–12	4–8	4–8	8–12
Distance to meadow edge (m)	34	73	80	135	106	79
Time of day						
6:00–9:00						
Minutes	205	291	292	212	184	279
Feedings	78	97	125	53	20	91
9:00–12:00						
Minutes	166	310	213	177	176	313
Feedings	84	98	62	35	42	91
12:00–15:00						
Minutes	290	217	380	146	176	322
Feedings	71	126	168	51	83	106
15:00–18:00						
Minutes	304	346	333	145	104	246
Feedings	68	84	111	54	32	86
18:00–21:00						
Minutes	230	223	97	194	117	97
Feedings	94	77	62	38	69	43

^aSee Figure 1 for numbers designating nests in Middle Perazzo Meadow.

at least 200 feedings at each of the six nests. Table 1 presents the dates and time each nest was under surveillance and the numbers of feedings by 3-hour period of the day.

Diet Analysis

To identify food items fed to nestlings, I examined the video with the video-editing software Wondershare Filmora9. I was conservative in my approach to identifying food items, not counting items of uncertain identity, which equaled 20% of all samples. Smaller food items were more difficult to identify than larger items. Other factors contributing to difficulty in identifying food items were the quick pace of feeding, obstructed views, and blurriness of the video. When possible, I identified each food item to order unless it could be adequately identified to a lower taxonomic level. Then I calculated the overall relative abundance and percent abundance for each category of prey for each nest and meadow. For Middle Perazzo Meadow, I combined the data from all five nests to obtain the overall relative abundance and percent abundance for the meadow. Finally, I quantified the relative abundance and percent abundance for each taxon during each of the five time periods for each nest site and meadow. Because of the low number of nests observed, I did not analyze the results statistically but present them descriptively.

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FIGURE 2. Willow Flycatcher feeding (A) butterfly (Lepidoptera) and (B) damselfly (Odonata) to nestlings.

Photo by Scott Dietrich

RESULTS

Diet Composition

In total, I identified 2277 individual food items representing 12 orders of arthropods delivered to nestlings in Lacey and Middle Perazzo meadows. The top taxa were the Diptera, Odonata, Ephemeroptera, Lepidoptera, and Raphidioptera (Table 2). The Diptera comprised species ranging in length from 9–14 mm (flesh flies, family Sarcophagidae, and hover flies, family Syrphidae) to 25–50 mm (horseflies, family Tabanidae, and crane flies, family Tipulidae). The Odonata consisted largely of damselflies (Figure 2) but also included a smaller number of dragonflies. The Ephemeroptera were represented largely by smaller mayfly species (likely genus *Ephemerella*) that emerged in the evening and occasionally during the middle part of the day. The Lepidoptera consisted of green moth caterpillars but also included a small number of medium and large adult butterflies and moths, while the Hymenoptera consisted mostly of small wasps (family Vespidae) ranging in length from 13 to 38 mm but also included a small number of bumblebees (genus *Bombus*). The Coleoptera were largely adult and larval ladybug beetles (family

TABLE 2 Numbers and Percentages of Arthropods Fed to Nestlings at Six Nests in Middle Perazzo and Lacey Meadows, Sierra Nevada

Order	Lacey <i>n</i>	Middle Perazzo ^a					Total	
		MP1 <i>n</i>	MP2 <i>n</i>	MP4 <i>n</i>	MP7 <i>n</i>	MP9 <i>n</i>	<i>n</i>	%
Diptera	167	74	163	41	26	74	545	24
Odonata	2	96	180	71	49	108	506	22
Ephemeroptera	3	12	57	72	100	123	367	16
Lepidoptera	25	142	50	20	19	23	279	12
Raphidioptera	118	120	7	0	2	30	277	12
Orthoptera	25	9	33	5	12	17	101	4
Hymenoptera	44	0	10	11	2	6	73	3
Coleoptera	7	12	22	0	8	8	57	3
Hemiptera	0	7	1	0	4	22	34	1
Trichoptera	4	2	1	7	4	1	19	1
Araneae	0	8	3	2	0	4	17	1

^aSee Figure 1 for numbers designating nests in Middle Perazzo Meadow.

Coccinellidae) but also included larger species. The Hemiptera consisted of leaf hoppers (family Cicadellidae), while the Trichoptera and Plecoptera consisted of species large for those orders, the October caddis, *Dicosmoecus atripes*, and western stonefly, *Calineuria californica*. The Araneae were not identified to species but included a variety of large and small spiders. The Raphidioptera were represented by snakeflies found in the Lodgepole Pine forest that surrounded both meadows.

Meadow and Territory Comparison

At Middle Perazzo Meadow the Odonata, Ephemeroptera, Raphidioptera, and Diptera constituted roughly 75% of the nestlings' diet, whereas at Lacey Meadow the Diptera and Raphidioptera alone combined to make up the same percentage (Figure 3). The Ephemeroptera, Odonata, and Lepidoptera predominated at Middle Perazzo, whereas the Raphidioptera, Diptera, and Hymenoptera predominated at Lacey. Percentages of the Coleoptera and Orthoptera were similarly low in both meadows. At one nest in Middle Perazzo Meadow, MP1, the percentages of Raphidioptera and Lepidoptera were much higher but the percentage of Ephemeroptera was much lower than at the other nests in that meadow (Figure 4). Also, at nest MP2 the percentage of Diptera was notably higher, and at nest MP7 the percentage of Ephemeroptera was notably higher than at the other nests in Middle Perazzo Meadow.

Daily Diet Comparison

The rate at which the nestlings were fed some categories of food items varied greatly during the day, while the rate for others varied little. At Lacey Meadow the Raphidioptera constituted 30–35% of the prey provided in the morning and late morning and 62% in the evening but no more than 8% in the afternoon and late afternoon. At Middle Perazzo Meadow the percentage of Raphidioptera varied only slightly through the day but was greatest in the morning (Figure 5). At both meadows the percentage of Diptera dropped considerably in the evening. By contrast, the Ephemeroptera were a minor constituent in the morning and late morning but made up a large percentage of the diet in the afternoon (27%) and evening (49%). For the Lepidoptera the percentage peaked in the late morning or early afternoon whereas for the Odonata it was fairly uniform through the day.

DISCUSSION

Meadow Diets

At both Lacey and Middle Perazzo meadows the arthropods fed to nestling Willow Flycatchers ranged from small terrestrial ladybugs to large aquatic dragonflies. Although the sample from the drier Lacey Meadow was small, it does help us understand the diversity possible in the Willow Flycatcher's diet in the Sierra Nevada. Results from all six nests pooled, 62% of the diet consisted of insects with aquatic life stages, but at the wetter Middle Perazzo Meadow, aquatic insects accounted for 80% of the diet. Although Lacey Meadow was mostly dry, the nestlings in the nest monitored there were nevertheless fed many Diptera that have early aquatic life stages (Erman 1984).

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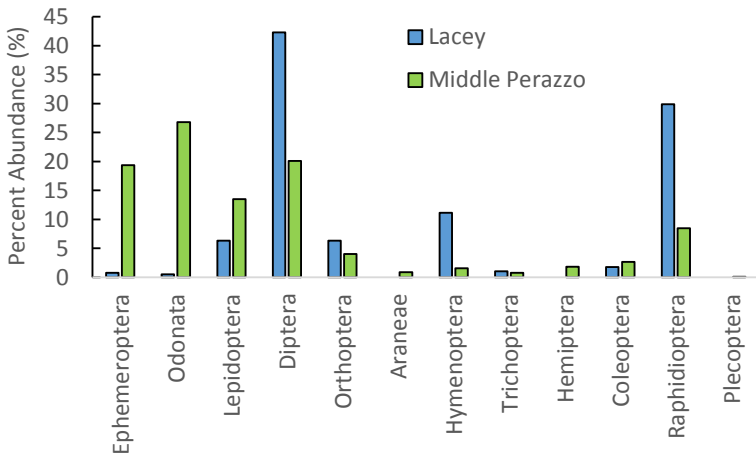


FIGURE 3. Percentage of each order of arthropods fed to nestling Willow Flycatchers at Lacey and Middle Perazzo meadows.

It is possible that these insects originated from small ponds that had dried up by early summer when I made my observations at Lacey Meadow. Diptera, abundant in both meadows, were a major constituent of the nestlings' diet at both meadows. Although odonates and mayflies were seldom provided at Lacey, they were a large part of the diet at Middle Perazzo, and I often saw them near ponds and river channels in the meadow, especially during peri-

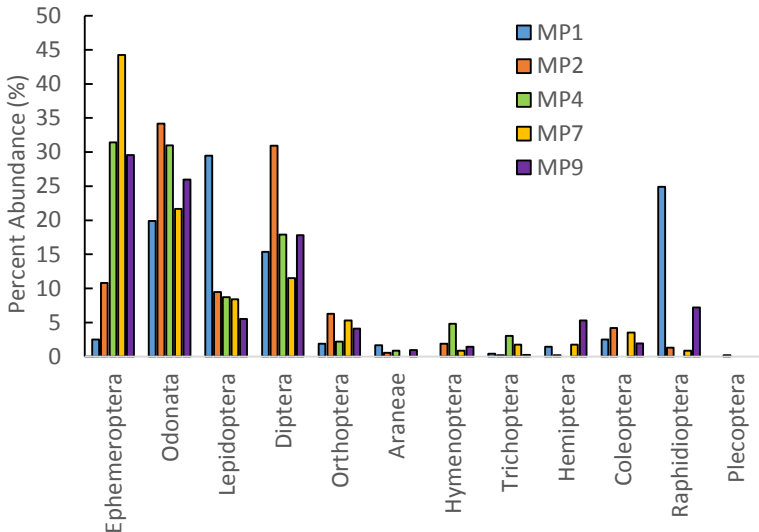


FIGURE 4. Percentage of each order of arthropods fed to nestling Willow Flycatchers at five nests in Middle Perazzo Meadow.

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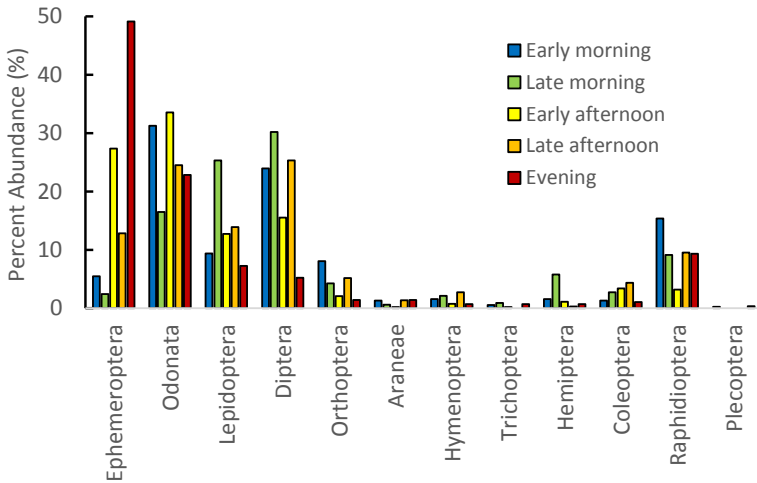


FIGURE 5. Percentage of each order of arthropods fed to nestling Willow Flycatchers in at five nests in Middle Perazzo Meadow by 3-hour periods of the day.

odic emergences and during ideal flying conditions. On multiple occasions I noted the nestlings being fed three or four mayflies or damselflies in a single delivery, as I have seen during mass emergences of caddisflies and stoneflies in other meadows of the Sierra Nevada (Dietrich 2020).

The large percentage of terrestrial food items at Lacey Meadow was surprising because the prey I had previously observed in Sierra meadows almost always consisted largely of aquatic insects (Dietrich 2020). Also, Willow Flycatchers prefer nesting near water (Serena 1982, Sanders and Flett 1989, Bombay et al. 2003). At the drier meadow the diet appeared to be dominated by pollinating Diptera, snakeflies, Hymenoptera (wasps, bumblebees), and Lepidoptera (adult moths and butterflies), plus grasshoppers. Vegetation around the nest monitored in Lacey Meadow comprised shrubby willows and large openings covered with wet meadow grasses and flowers. Wet-meadow flowers such as Ranger’s Buttons (*Sphenosciadium capitellatum*) appeared to be especially important, as I noted many different pollinating insects on the flower heads, and flycatchers selectively gleaning food items from them. The nearby conifer forest also appears to be important as the source of snakeflies on which I often saw flycatchers foraging in the morning and evening near the nest in Lacey Meadow. At Middle Perazzo Meadow Willow Flycatchers also foraged on terrestrial arthropods outside of the meadow in the conifer forest and sagebrush habitat, but apparently less often than in Lacey Meadow and in the morning only. Other terrestrial prey such as ladybug beetles (adults and larvae), leaf hoppers, and lepidopteran caterpillars appear to be associated with wetland vegetation (*Carex*, *Juncus*, *Salix*) in Middle Perazzo Meadow; I often observed the flycatchers gleaning them from such plants.

Differences in the type of herbaceous vegetation, availability of water, and the distance to the meadow’s edge appear to be responsible for differences in the diet between Lacey and Middle Perazzo meadows. The wetter conditions

in Middle Perazzo Meadow likely led to the higher percentage of damselflies, dragonflies, and mayflies there, whereas the drier environment in Lacey Meadow was likely responsible for the greater proportion of terrestrial prey in the diet there. The nearness of the nest monitored in Lacey Meadow to the meadow's edge probably made it easier for Willow Flycatchers to forage for snakeflies than at Middle Perazzo Meadow, where the surrounding forest was generally farther from the nests.

The observed variation at Middle Perazzo Meadow appears to be due mostly to the nest's location within the meadow. Both nests MP1 and MP2 were situated closer to the meadow's edge with its large numbers of snakeflies, grasshoppers, and Diptera. Conversely, at nests MP4 and MP7, located farther from the meadow's edge, the percentages of damselflies, dragonflies, and mayflies were higher but those of terrestrial prey were lower. The composition of the diet within a meadow may vary with the nest's distance to water and various terrestrial habitats. With a larger sample of nests these hypotheses could be evaluated with statistical modeling.

Diurnal Diet Variation

The variation in nestling Willow Flycatchers' diets through the day reflects not only the fluctuation through the day in prey available to the birds but also changes in the adults' foraging behavior. The high proportion of mayflies provided in the afternoon and evening presumably coincides with their increased availability during mass emergence. During these emergences flycatchers could be observed selectively targeting mayflies from the same foraging perches at high rates, suggesting an abundance of these food items was available during this time of the day. The increase in provisioning with snakeflies in the morning and evening coincided with an increase in foraging outside of the meadow. In Lacey Meadow I observed Willow Flycatchers foraging selectively on pollinating insects that had concentrated near flowers in the afternoon when conditions for pollinating may have been better. An observed increase in leaf hopper activity in the late morning appeared to coincide with the increase in the number of leaf hoppers fed to nestlings at that time. I have witnessed similar diurnal patterns in nestlings' diets and adult flycatchers' foraging in other Sierra meadows. The apparent consistency in provisioning with Odonata and Diptera through the day may reflect uniform availability. Given that the availability of various prey may fluctuate through the day, future studies should sample evenly through the day to ensure that samples are representative.

Diet Comparison

The diet of *E. t. brewsteri* I observed appears to differ from that of *E. t. extimus* in the Southwest but may be similar to that of *E. t. adastus* in the Great Basin. The percentages of Coleoptera and Hymenoptera I observed were lower than those found in the Southwest by DeLay et al. (2002), Drost et al. (2003), Wiesenborn and Heydon (2007), and Durst et al. (2008). Diptera appear to be important in all areas where the Willow Flycatcher's diet has been studied. Lepidopteran caterpillars appear to be more important in Sierra meadows than in the Southwest, but I found them being fed in

similar numbers in northern Utah (unpubl. data). Emergent insects such as the Ephemeroptera, Trichoptera, and Plecoptera have not been found in the diet of *E. t. extimus*, but my preliminary observations suggest that they may be more important to *E. t. adastus*. In the Sierra Nevada I observed Willow Flycatchers feeding on large numbers of Odonata, but in the Southwest they have been reported as only moderately important at a few sites. I found Orthoptera abundant in the diets of *E. t. adastus* in northern Utah, but they have been little reported in the diet of *E. t. extimus*. Snakeflies have not been reported in the Willow Flycatcher's diet outside of the Sierra Nevada (Beal 1912, Bent 1942, DeLay et al. 2002, Drost et al. 2003, Wiesenborn and Heydon 2007, Durst et al. 2008). Other food items such as spiders reported as important in the diet of *E. t. extimus* I seldom found being eaten in the Sierra Nevada. However, because of the small number of meadows sampled in my study these inferences are preliminary.

Management and Restoration Implications

Proper management of meadows that Willow Flycatchers occupy can benefit production of the birds' prey. Simply eliminating grazing within and near meadows during the breeding season allows an increase in the abundance of the grass, forbs, and wetland vegetation to which many Hymenoptera, Diptera, Lepidoptera, and grasshoppers are attracted. Thinning or removal of trees near meadows may disfavor terrestrial food insects such as snakeflies that are reliant on the conifer forest surrounding the meadows. Thinning of conifer forests that closely surround meadows the flycatchers may occupy should be done with caution. Many of these meadows are situated near reservoirs that often allow for control of flooding within the meadows. If a reservoir's level can be maintained to create more aquatic habitat, production of aquatic food insects should increase. Managers of these reservoirs should seek to keep meadows flooded at least through the early part of the summer, and longer if possible, to optimize the meadows' production of aquatic food.

Meadow restoration in the Sierra Nevada is often focused on restoring the Willow Flycatcher's nesting habitat but can unintentionally degrade foraging habitat. Restoration of a meadow should enhance habitat features such as ponds, streams, and vegetation that are directly or indirectly responsible for the meadow's production of food. Determining whether a meadow has the habitat necessary to support production of sufficient food should be the first step in developing a restoration plan, especially if the plan's goal includes establishing conditions suitable for the Willow Flycatcher. For example, some meadows may be food-limited because their streams are degraded and can no longer support reproduction of mayflies, caddisflies, and stoneflies, or ponds have dried up and no longer support production of damselflies, dragonflies, and some Diptera. Restoration of these habitat features should be done without damaging features of nesting habitat such as shrubby willows. Additionally, meadow-restoration projects should seek to restore the physical processes of flooding and sediment transport that are responsible for creating and maintaining the ponds and wetland vegetation that are so important to producing the Willow Flycatcher's food in the Sierra Nevada.

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ACKNOWLEDGMENTS

I thank Peter Wilcock, Frank Howe, and Karin Kettenring from Utah State University for their support and guidance in research and writing the manuscript. Helen Bombay provided guidance, expertise, and support of field work. Thanks to Ed Pandolfino who generously offered his time to edit the final manuscript and for his encouragement and guidance through the publishing process. Also, thanks to my *Western Birds* reviewers for improving the final draft.

LITERATURE CITED

- Beal, F. E. L. 1912. Food of our more important flycatchers. U.S. Bureau Biol. Surv. Bull. 4; <https://doi.org/10.5962/bhl.title.62957>.
- Bent, A. C. 1942. Life histories of North American flycatchers, larks, swallows, and their allies. U.S. Natl. Mus. Bull. 179.
- Bombay, H. L., Morrison, M. L., and Hall, L. S. 2003. Scale perspectives in habitat selection and animal performance for Willow Flycatchers (*Empidonax traillii*) in the central Sierra Nevada, California. *Studies Avian Biol.* 26:60–72.
- DeLay, L. S., Stoleson, S. H., and Farnsworth, M. 2002. A quantitative analysis of the diet of Southwestern Willow Flycatchers in the Gila Valley, New Mexico. Final report to T&E, Inc.; https://www.fws.gov/southwest/es/arizona/Documents/SpeciesDocs/SWWF/Scoping_PCH/37_0-017%20R1.pdf.
- Dietrich, S. E. 2020. Habitat, diet, and foraging ecology of Willow Flycatcher in Sierra Nevada meadows. Master's thesis, Utah State Univ., Logan.
- Drost, C. A., Paxton, E. H., Sogge, M. K., and Whitfield, M. J. 2003. Food habits of the Southwestern Willow Flycatcher during the nesting season. *Studies Avian Biol.* 26:96–103.
- Durst, S. L., Theimer, T. C., Paxton, E. H., and Sogge, M. K. 2008. Age, habitat, and yearly variation in the diet of a generalist insectivore, the Southwestern Willow Flycatcher. *Condor* 110:514–525; <https://doi.org/10.1525/cond.2008.8493>.
- Erman, N. 1984. The use of riparian systems by aquatic insects, in *California Riparian Systems: Ecology, Conservation, and Productive Management* (R. E. Warner and K. Hendrix, eds.), pp. 177–182. Univ. of Calif. Press, Berkeley.
- Green, G. A., Bombay, H. L., and Morrison, M. L. 2003. Conservation assessment of the Willow Flycatcher in the Sierra Nevada. U.S. Forest Service, Vallejo, CA; <https://www.sierraforestlegacy.org/Resources/Conservation/SierraNevadaWildlife/WillowFlycatcher/WF-Green03.pdf>.
- Harris, J. H., Sanders, S. D., and Flett, M. A. 1987. Willow Flycatcher surveys in the Sierra Nevada. *W. Birds* 18:27–36.
- Loffland, H. L., Schofield, L. N., Siegel, R. B., and Christman, B. 2022. Sierra Nevada Willow Flycatcher decline continues but losses abate at two restored meadows. *W. Birds* 53:52–69; <https://doi.org/10.21199/WB53.1.5>.
- Sanders, S. D., and Flett M. A. 1989. Ecology of a Sierra Nevada population of Willow Flycatchers (*Empidonax traillii*), 1986–1987. Calif. Dept. Fish and Game, Wildlife Mgmt. Div., Nongame Bird and Mammal Section, Sacramento.
- Serena, M. 1982. The status and distribution of the Willow Flycatcher (*Empidonax traillii*) in selected portions of the Sierra Nevada, 1982. Calif. Dept. Fish and Game, Wildlife Mgmt. Branch Admin. Rep. 82-5.
- Wiesenborn, W. D., and Heydon, S. L. 2007. Diets of breeding Southwestern Willow Flycatchers in different habitats. *Wilson J. Ornithol.* 119:547–557; <https://doi.org/10.1676/06-101.1>.

Accepted 11 February 2022
Associate editor: Kenneth P. Able