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Habitat, Diet, and Foraging Ecology of Willow Flycatcher in Sierra Nevada Meadows

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HABITAT, DIET, AND FORAGING ECOLOGY OF WILLOW FLYCATCHER IN SIERRA NEVADA MEADOWS

by

Scott E. Dietrich

A thesis submitted in partial fulfillment
of the requirements for the degree

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ABSTRACT

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Major Professor: Dr. Peter Wilcock
Department: Watershed Sciences

The last stronghold of the California Willow Flycatcher (*Empidonax traillii*) population, which exists in the Sierra Nevada, continues to decline, necessitating a clearer understanding of how meadows provide habitat for the species. To gain this understanding, we assessed vegetation type, saturation levels, and invertebrate species at 51 different sites within four meadows located in the Little Truckee River drainage. 17 of these sites were occupied by nesting Willow Flycatcher during the time of the study, 17 sites had been occupied by nesting Willow Flycatcher in annual surveys between 1997 and 2010 but are no longer used, and 17 sites had never been used by nesting Willow Flycatcher. We found that occupied sites were generally far wetter than unused sites. Total saturation varied from 88% to 100% and total inundation varied from 20% to 52%. Sedge vegetation coverage was also much higher in occupied sites than unused sites and varied from 62% to 90%. Abandoned sites were found to not be suitable for breeding Willow Flycatcher because they were either too dry (low food abundance) or they were too wet (decreased shrub quality). Food items desired by Willow Flycatcher were found

to be higher in abundance within wetter occupied sites compared to drier unused sites. In addition to evaluating vegetation coverage, saturation levels, and invertebrates, we examined Willow Flycatcher diet, foraging behavior, and food/habitat relationships by using video footage of nestlings being fed and field observations. Over 75% of the Willow Flycatcher diet was represented by Lepidoptera (moth caterpillar), Raphidioptera (snakefly), Ephemeroptera (mayfly), Odonata (dragonfly and damselfly), and Hemiptera (leafhopper). Aquatic invertebrate food items composed 42% of the diet and aquatic habitat features such as stream channels and oxbow ponds were found to be important. Overall, gleaning and hawking foraging methods were used relatively equally, 49% and 51% of the time, respectively. Foraging often took place outside of territory boundaries and some food items, such as Raphidioptera, were caught outside of meadow boundaries. Diets and foraging behavior also varied throughout the day with some food items, such as Ephemeroptera and Lepidoptera, being targeted only during certain times of the day.

(71 pages)

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The last stronghold of the California Willow Flycatcher (*Empidonax traillii*) population, which exists in the Sierra Nevada, continues to decline, necessitating a clearer understanding of how meadows provide habitat for the species. To gain this understanding, we assessed vegetation type, saturation levels, and invertebrate species at 51 different sites within four meadows located in the Little Truckee River drainage. 17 of these sites were occupied by nesting Willow Flycatcher during the time of the study, 17 sites had been occupied by nesting Willow Flycatcher in annual surveys between 1997 and 2010 but are no longer used, and 17 sites had never been used by nesting Willow Flycatcher. We found that occupied sites were generally far wetter than unused sites. Total saturation varied from 88% to 100% and total inundation varied from 20% to 52%. Sedge vegetation coverage was also much higher in occupied sites than unused sites and varied from 62% to 90%. Abandoned sites were found to not be suitable for breeding Willow Flycatcher because they were either too dry (low food abundance) or they were too wet (decreased shrub quality). Food items desired by Willow Flycatcher were found to be higher in abundance within wetter occupied sites compared to drier unused sites. In addition to evaluating vegetation coverage, saturation levels, and invertebrates, we examined Willow Flycatcher diet, foraging behavior, and food/habitat relationships by using video footage of nestlings being fed and field observations. Over 75% of the Willow Flycatcher diet was represented by Lepidoptera (moth caterpillar), Raphidioptera

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Scott Dietrich

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CHAPTER I

INTRODUCTION

Successful restoration and management of Willow Flycatcher habitat in Sierra Nevada meadows depends on a clear understanding of habitat requirements. Why Willow Flycatcher are selectively nesting in certain locations within Sierra Nevada meadows is a question that remains unanswered by those with the responsibility of protecting and restoring Willow Flycatcher in Sierra Nevada meadows today (Bombay et al. 2003). Part of the difficulty in determining habitat requirements is due to the lack of strong evidence for the role of water within Willow Flycatcher habitat. Previous studies have provided quantitative evidence for the nature and extent of willow shrubs, but not for nature and extent of water and saturated soil (Serena 1982, Bombay et al. 2003).

If Willow Flycatcher choose wetter locations for their nests, then what ecological advantage does this provide? Willow Flycatcher may choose wetter locations because of increased availability of aquatic insects for food. If true, diet and foraging behavior should provide evidence for the need of aquatic habitat. Willow Flycatcher are observed to nest and forage in meadows. In the absence of detailed diet and foraging information, diets in Sierra Nevada meadows have been assumed to be similar to diets found in other parts of North America (Green et al. 2003). Because meadows in the Sierra Nevada may well have distinct hydrologic and vegetative conditions, it cannot be assumed that the diets of Willow Flycatcher in Sierra Nevada meadows are similar to those found in non-meadow habitat outside of the Sierra Nevada.

In Chapter Two, we investigate the relationship between water, herbaceous vegetation community, and food production within three different occupancy types

(occupied, abandoned, unused). Occupied sites hosted an active nest with a breeding pair during the 2017 field season. Abandoned sites had Willow Flycatcher occupation observed during annual surveys between 1996 and 2008, but were no observed to be used between 2016 and 2019, Unused sites have had no observed nesting activity. We wanted to know whether wetness level, herbaceous vegetation type, and food production (arthropod abundance) differ among active sites, abandoned sites, and unused sites. We also wanted to know whether relationships exist between wetness level, herbaceous vegetation, and overall food production. Evaluating why once occupied sites have been abandoned can give insight into essential habitat attributes.

In Chapter Three, I use video footage of adults feeding nestlings and observations of Willow Flycatcher foraging to evaluate their diet and foraging behavior in meadows of the Sierra Nevada. Of particular interest is the fraction of Willow Flycatcher diet that is aquatic based. In addition to identifying important food items, also useful is a description the foraging behavior in meadows and whether distinct foraging patterns exist. In combination, these observations link food and habitat relationships and support conclusions regarding the importance of aquatic habitat features such as streams and floodplains. This information into diet and foraging behavior of Willow Flycatcher will give further insight into what habitat features and conditions are needed to support food production within Sierra Nevada meadows.

A better understanding of the role of wet habitat will help managers protect existing habitat and restore habitat to meadows that currently do not support nesting Willow Flycatcher. The urgency for a more complete understanding of Willow

Flycatcher habitat requirements, diet, and foraging behavior is motivated by the delicate state of the current Willow Flycatcher population in the Sierra Nevada.

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CHAPTER II

HABITAT REQUIREMENTS OF WILLOW FLYCATCHER IN SIERRA NEVADA MEADOWS

INTRODUCTION

Few other Sierra birds are as specialized in their choice of habitat as the Willow Flycatcher (*Empidonax traillii*) (Beedy and Pandolfino 2013). Serena (1982) described Willow Flycatcher habitat in the Central and Northern Sierra as wet meadows lined with willows and alders, whereas Sawyer and Keeler-Wolf (1995) classified their habitat as "montane wetland shrub habitat". Saturated conditions within meadows can provide both aquatic food production and protection from terrestrial predators (Green et al. 2003). Protection from terrestrial predators has been previously studied in the Sierra Nevada but results did not show a relationship between nest predation and territory saturation (Cocimano et al. 2011). Aquatic food production has not been studied in Sierra Nevada meadows. A connection between food production and territory wetness, along with documentation of the hydrologic conditions for active territories, are needed as evidence for why Willow Flycatcher appear to choose wetter portions of meadows as habitat. Such information could help define habitat targets for meadow restoration in the Sierra Nevada.

The need to fully understand Willow Flycatcher habitat and its relationship to water has never been greater. Recent demographic studies in the Sierra Nevada show that the Willow Flycatcher population continues to decline and populations that were once thought to be strongholds have been severely diminished or completely extirpated (Green et al. 2003, Siegel et al. 2008, Mathewson et al. 2013). Previous studies of Willow

Flycatcher habitat have not been able find a direct connection between saturation level and occupancy of a meadow or areas within a meadow, making it difficult to determine whether water is a requirement of Willow Flycatcher habitat (Serena 1982, Bombay et al. 2003). Although no direct connection has been made between saturation level and meadow occupancy, many studies have found high saturated levels within active territories occupied by Willow Flycatcher (Serena 1982, Sanders and Flett 1989, Bombay et al. 2003).

In this study we focus on evaluating saturation conditions and food production among sites that were actively occupied by nesting birds during the field season, sites that had previously been occupied but appear to no longer be used, and sites that have never had observed nesting. We also evaluate herbaceous vegetation cover across the different sites. The field area for this study is in the drainage of the Little Truckee River. Willow Flycatcher surveys were conducted in the area from 1997 to 2010 and then repeated for this study in 2017. The long history of WIFL observation in the study sites allows a richer examination of habitat requirements than possible based on a single survey of active territories.

Our study was organized around three broad questions: 1) Do unique wetness and herbaceous vegetation conditions exist within occupied sites? 2) Does food production differ between the three occupancy types? 3) Why are some sites no longer occupied and does this relate to changes in hydrologic and vegetative condition? By improving our understanding of hydrologic and herbaceous vegetation components of Willow Flycatcher habitat, we hope to define preferred habitat requirements, including supporting evidence for these essential functions.

STUDY AREA

Willow Flycatcher nesting surveys and habitat observations were made in three meadow systems of the Little Truckee River watershed in the northern portion of the Sierra Nevada, approximately 20 miles north of Truckee, California (Figure 2.1). Lacey Valley, Perazzo Meadow, and Little Truckee River meadows are in a mountainous area on the east slope of the Sierra Nevada at elevations ranging from 6,400 to 7,000 feet. Lacey Valley and Perazzo Meadow are large, wide single meadows and the Little Truckee River Meadow is a multi-meadow system characterized by two large (long) meadows (upper and lower) separated by a narrow, confined bedrock valley. The three meadows are typical of other meadows in the Sierra Nevada formed by past glacial activity and characterized by large flat valleys (Wood 1975). The meadow soils are dominated by fine grained alluvial sediments and organic material with high levels of soil moisture (Balance 2013, Swanson 2009, Wood 1975). Vegetation within the meadows is mostly sedge (*Carex sp.*), grass, forbs, and willow shrubs (*Salix sp.*) with some aquatic species found in abandoned channel ponds. Willow shrubs are often the only woody species found within the meadows, but some drier locations have lodgepole pine (*Pinus contorta*) and occasional sagebrush shrubs (*Artemisia*).

Precipitation within the watershed is dominated by winter snow that melts in early summer, causing rivers to flood adjacent meadows. Meadows often have abandoned channels and ponds that are filled with water during snowmelt but go dry by the late summer (Sanders and Flett 1989). Late summer river baseflow is typically maintained by groundwater sources (Balance 2013, Swanson 2009, Wood 1975). The flooded extent of each meadow varies by year, with portions that flood annually, portions that never flood,

and portions that flood only in years with above average snowmelt. Rivers in the three meadow systems are high energy, with a meandering pattern and active sediment transport during spring snowmelt, with occasional low-energy meandering and anastomosing segments. Tributaries produce some small alluvial fans on the margins of the three meadows that typically have shallow multichannel networks often maintained by seeps.

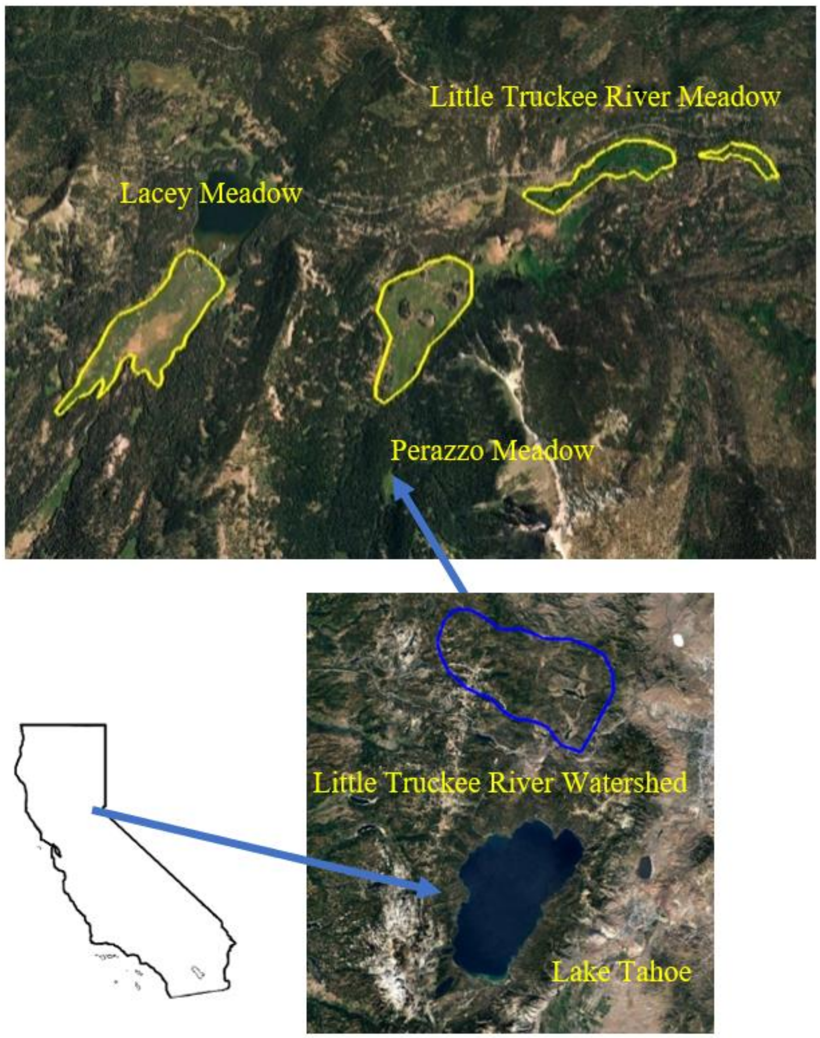

Figure 2.1. Study area, Little Truckee River watershed, Tahoe National Forest. Photo Credit, Google Earth.

METHODS

Bird Surveys

Willow Flycatcher bird surveys were conducted in the summer of 2017 from June 1 to July 25 from sunrise to 10:00 AM. Our 2017 surveys used the same survey method and transects established for breeding surveys conducted from 1997 to 2010 (Bombay et al. 2003). All sites were surveyed twice during the breeding season, including a survey during June 15 to June 25, when all nesting birds were expected to have arrived. The second survey was conducted either during the early breeding season June 5 to June 14 or later in the season between June 26 to July 15. Meadows were surveyed by walking established transects set out by Bombay et al. (2003) and stopping at points evenly spaced along the transect to look and listen for Willow Flycatcher. At each point along the transect, we broadcast a recording of Willow Flycatcher song and calls for six minutes and then observed and listened for the presence of Willow Flycatcher. If a Willow Flycatcher was detected within this time interval, or after, subsequent follow-up surveys were used to determine whether the flycatcher were acting territorial and using the area for nesting purposes. Follow-up surveys were important to determine if flycatcher spotted during the initial survey was nesting and not simply migrating through. Once a Willow Flycatcher was determined to be on an established territory, the spatial extent of the territory was mapped by observing where the male Willow Flycatcher was actively defending and where male and female flycatcher were actively foraging. A foraging buffer was added to the defended territory when foraging outside of the defended territory was frequent and may be important for supporting the Willow Flycatcher family (Sanders and Flett 1989). Delineation of an expanded foraging buffer

was informed by typical limits defined for acceptable Willow Flycatcher habitat (Green et al. 2003).

Occupancy Types

Seventeen occupied sites were found during the 2017 survey. In order to compare habitat conditions with unused and abandoned sites, 17 of each of those sites were defined and surveyed in 2017 for a total of 51 surveyed sites.

Occupied Site

A survey area was considered to be occupied if a male Willow Flycatcher was found to be exhibiting territorial behavior (e.g. singing or physically defending the site). The only criteria for occupancy was the presence of a male displaying territorial behavior. Presence of a female or nest was not needed for occupancy determination. Follow up visits were used to determine if Willow Flycatcher observed during the initial survey had successfully established a territory. All occupied sites and their boundaries were recorded with GPS and mapped using GIS software.

Abandoned Site

An abandoned site is an area occupied at least twice during the 1997-2010 survey period but not occupied in 2017 survey period. Some site records included nest location but did not have defined information (geographical data) on territory boundaries. In these cases, territory boundaries were estimated based on observed Willow Flycatcher habitat characteristics and defined willow shrub abundance standards (Green et al. 2003). All of the abandoned site polygons were within the area that was previously surveyed and therefore already deemed to be potential Willow Flycatcher habitat by 1997-2010 survey.

Unused Site

An unused site is an area within a meadow that has been determined to be potential habitat (thought to be possible habitat in 1997-2010 survey) but has not been occupied during both the 1997-2010 survey period and the 2017 survey. These areas were identified based on defined willow shrub attributes for Willow Flycatcher habitat and were located along transects set out during 1997-2010 survey period. Locations that were significantly changed (shrub and hydrological changes) by recent restoration projects were not used in the study. Willow shrubs within established unused sites were field verified to make sure that they met shrub foliar density and shrub coverage standards set out by other studies of Willow Flycatcher habitat (Sanders and Flett 1987, Fowler et al. 1991, Scully 1995, Bombay et al. 2003). In addition, unused site size was based on the average size for occupied sites established in the 2017 survey. Each unused site was field verified to confirm that they were not located in areas that were obviously incongruent with geomorphic conditions found in both occupied and abandoned sites. Further, each unused site was confirmed to be absent of significant encroachment by conifers, which are thought to deter Willow Flycatcher nesting (Bombay et al. 2003, Green et al. 2003).

Hydrologic Sampling

Hydrologic surveys were conducted during the latter part of the 2017 breeding season (mid-July to late-July) in order to determine inundation and wetness levels when resources are in the greatest demand for nesting. All sites were surveyed along five equally spaced transects established perpendicular to a single transect spanning the longest portion of the location boundary polygon. Ten equally spaced survey points were established on each of the five perpendicular transects, for a total of 50 survey points for

each site. At each survey point, a modified version of the “squishy boot” test (Rinderer et al. 2012) was applied to an area of 1 m^2. The test seeks to describe the different hydrologic conditions within the meadow by selecting from five different hydrologic types with different inundation levels, vegetation types, and soil wetness (Table 2.1, Figure 2.2).

Hydrologic Survey (“Squishy Boot” Test)

The “squishy boot” test is a three-step process. First, the surveyor determines if standing water is present above the ground surface. If standing water is more than 0.5 ft. above the ground surface (approximately above the ankle), then the class depends on whether emergent herbaceous vegetation is present or not. If vegetation is present, then the area is categorized as deep inundation with vegetation (WV). If vegetation is not present, the area is categorized as deep inundation without vegetation (WOV). If the level of standing water is below the surveyor’s ankle, the area is shallow inundation. If standing water is not present above the ground surface, the water content of the soil is measured by kneeling on exposed soil with most of one’s body weight on one knee. For optimal results, the surveyor stays kneeling for a full minute. If after one minute the knee is wet or shows moisture on the pant leg, then the area is classified as wet soil type. If not, the soil is classified as dry soil. It is important to conduct this last step during the middle part of the day to avoid wet pants from morning dew. The percent area covered by each hydrologic type within each 1 m^2 survey area is recorded. An average hydrologic type distribution is then found for each site and then further for each occupancy type.

Table 2.1. Hydrologic type description and associated herbacious vegetation community. Soil saturation is the point where the soil can no longer absord or hold any more water.

HYDROLOGIC TYPES	DEFINITION	HERBACEOUS VEGETATION COMMUNITY
Deep Inundation (WOV)	Areas that have water inundation depths greater than .5 feet (6 inches) and no vegetation present	Aquatic
Deep Inundation (WV)	Areas that have water inundation depths greater than .5 feet (6 inches) and have emergent herbaceous vegetation present	Hydric
Shallow Inundation	Areas that have less that .5 feet (6 inches) of water inundation and have emergent herbaceous vegetation present. Areas that do not have standing water but soils are saturated are also included	Hydric/Mesic
Wet Soil	Areas that are not saturated or inundated with water but do have some level of wetness within the soil	Mesic
Dry Soil	Area that are not saturated or inundated with water and do not have any level of wetness in the soil	Xeric

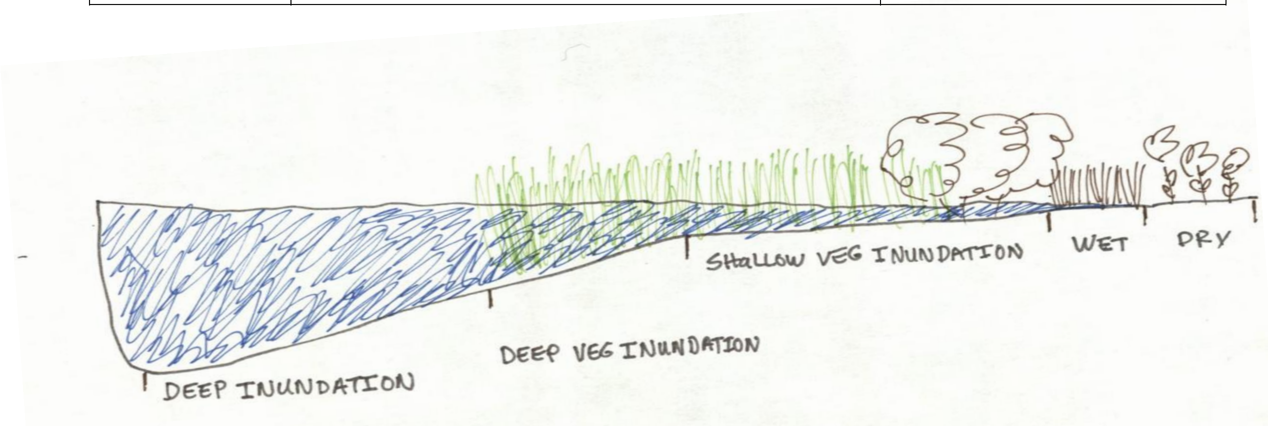

Figure 2.2. Cross section of an oxbow pond showing hydrologic types. Deep Inundation indicates deep water with no vegetation, Deep Veg Inundation is deep water with emergent herbaceous vegetation, Shallow Veg Inundation is shallow water with emergent herbaceous vegetation and willow shrubs, Wet is wet soil with grass/forbs, and Dry is dry soil with grass/forbs.

Hydrologic Metrics

Along with hydrologic type distribution for each occupancy type, two hydrologic metrics (Total Saturation, Total Deep Inundation) were used to better describe the overall hydrologic conditions within each site (Table 2.2). Each hydrologic metric was found by combining different hydrologic types.

Table 2.2. Hydrologic metric descriptions for sites in meadows of the Little Truckee River watershed.

HYDROLOGIC METRICS	DEFINITION	APPLICATION
Total Saturation	The total area that is inundated with water or has soil that is fully saturated.This is the combination of shallow inundation and both deep inundation hydrologic types (WOV and WV).	Used to determine the area that is flooded during a given year
Total Deep Inundation	The total area that is inundated with water greater than .5 feet (6 inches). This is the combination of both deep inundation hydrologic types (WOV and WV).	Used to determine deep abandoned channels or pond areas

Herbaceous Vegetation Sampling

Herbaceous vegetation sampling took place in the first two weeks of August 2017, after flycatcher hatchlings had fledged. Each location was sampled for four herbaceous vegetation types: sedge, rush, grass, and forbs. Individual species within each herbaceous vegetation type were not determined for the sake of efficiency, and because many vegetation types such as sedge and rush are often limited to just a few species in Sierra Nevada meadows (Ratliff 1982). Sedge vegetation communities were usually dominated by Nebraska Sedge (*Carex nebrascenses*).

Herbaceous Vegetation Survey

Herbaceous vegetative surveys were conducted at all sites using the same five transects deployed for the hydrologic surveys, but points were taken only at five evenly spaced locations along each of the five transects, giving a total of 25 survey points for each survey site. At each point, the percent coverage for each vegetation type was determined within a 1 m^2 area using visual estimates of each vegetation type and recorded 0-25%, 25-50%, 50-75%, 75-100%.

Food Sampling

Food or arthropod sampling was performed for all sites in the first two weeks of August 2017. The purpose of the food sampling was to determine whether food abundance was different within the occupancy types and to evaluate whether food abundance was related to total saturation and herbaceous vegetation type. Sampling for food was conducted by sweeping a net back and forth within a buffer zone of three feet around willow shrubs within each site polygon territory boundary. The sweeping lasted three minutes and was done at an even walking pace in order to survey as much of the willow shrub buffer feeding zone as possible. Sweeping surveys were conducted once. The food samples were stored in a freezer within zip lock plastic bags and later examined at the BLM National Aquatic Monitoring Center at Utah State University.

Food Metrics

Total Willow Flycatcher relative food abundance and total food abundance were used as metrics to determine the relative abundance and type of food found at each site. To better understand the type of food used by Willow Flycatcher, a separate study using direct video observation of Willow Flycatcher nests was used to evaluate food items consumed by Willow Flycatcher (Chapter 3). Only food items observed to be consumed by Willow Flycatcher adults and hatchlings were used to determine total Willow Flycatcher food relative abundance. Total Willow Flycatcher relative food abundance is the percent of food base that is available for Willow Flycatcher and includes Odonata, Hymenoptera, Diptera, Trichoptera, Ephemeroptera, and Hemiptera. Total food abundance included all food items collected within each site which includes both Willow Flycatcher food and all other food items sampled.

RESULTS

Occupancy Types

Only two of the four meadows surveyed were occupied by Willow Flycatcher in 2017. Perazzo Meadow had six occupied sites and Little Truckee River 1 Meadow had eleven occupied sites. Abandoned sites were surveyed in Perazzo Meadow (6), Little Truckee River 1 Meadow (6) and Little Truckee River 2 Meadow (5). Unused sites were defined in all four meadows: Perazzo Meadow (3), Little Truckee River 1 Meadow (3), Little Truckee River 2 Meadow (5), Lacey Meadow (5).

Hydrologic Analysis

Occupied sites had a mean total saturation of 97% (range = 88% to 100%) with 62% shallow inundation and 35% deep inundation (17% WOV and 18% WV) (Figure 2.3, Table 2.3). The remaining occupied area was 3% wet soil. Unused sites had a total saturation of 24% (range = 0% to 73%) with 22% shallow inundation and 2% deep inundation (1% deep inundation WOV and 1% deep WV). The remaining 76% of the unused site area was 36% wet soil and 38% dry soil. Abandoned sites had a total saturation of 65% (range = 0% to 100%) with 44% shallow inundation and 21% deep inundation (12% WOV and 9% WV). The remaining 35% was wet soil at 17% and dry soil at 18%.

Total saturation for occupied sites was statistically different from unused sites (Wilcox function and Mann-Whitney statistical test, P-value <0.02) but not from abandoned sites (Figure 2.4, Table 2.3). Ten abandoned sites had total saturation within the range observed for occupied sites (88% to 100%) and seven within unused sites (0% to 73%). Total deep inundation ranged from 20 to 52% for occupied sites, while unused

sites ranged from 0% to 8% (Figure 2.5). There was a statistical difference in deep inundation for occupied and unused sites (P-value <0.02) but abandoned sites were not statistically different from unuused and occupied sites (Table 2.3).

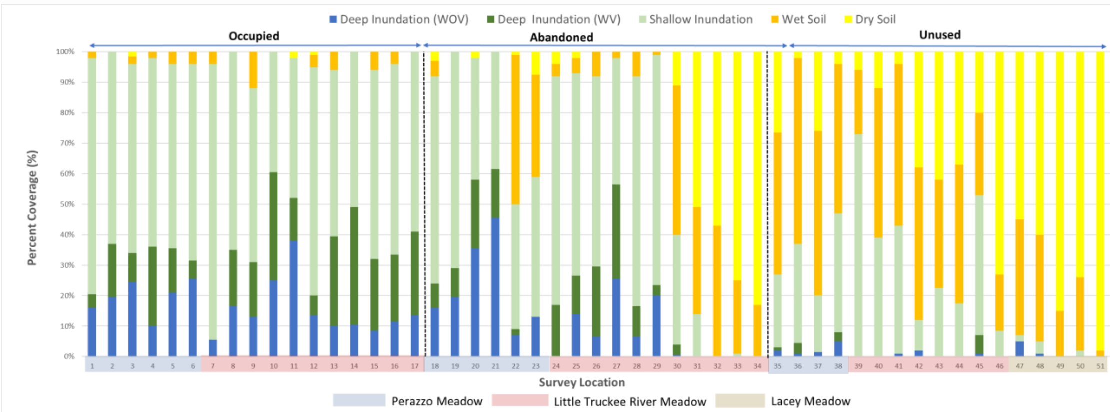

Figure 2.3. Distribution of hydrologic type coverage (%) for occupied, abandoned, and unused sites for Little Truckee River waterhsed (n= 51 surveyed sites).

Table 2.3. Hydrologic type results for occupied, abandoned, and unused sites for the Little Truckee River waterhsed.

	Occupied (O)			Abandoned (A)			Unused (U)			*P-Value*		
VARIABLE	Mean	S.D	Range	Mean	S.D	Range	Mean	S.D	Range	O vs.U	O vs. A	U vs. A
Deep Inundation (WOV) %	17	8	32, (6 - 38)	12	14	46, (0 - 46)	1	2	5, (0 - 5)	<.02	0.13	<.02
Deep Inundation (WV) %	18	11	38, (0 - 38)	9	10	31, (0 - 31)	1	2	6, (0 - 6)	<.02	<.02	<.02
Shallow Inundation %	62	12	51, (40 - 91)	44	27	76, (0 - 76)	22	20	73, (0 - 73)	<.02	0.11	<.05
Wet Soil%	3	3	12, (0 - 12)	17	18	49, (0 - 49)	36	17	59, (2 - 61)	<.02	<.02	<.02
Dry Soil %	0	1	2, (0 - 2)	17	29	83, (0 - 83)	39	31	96, (2 - 98)	<.02	<.02	<.02

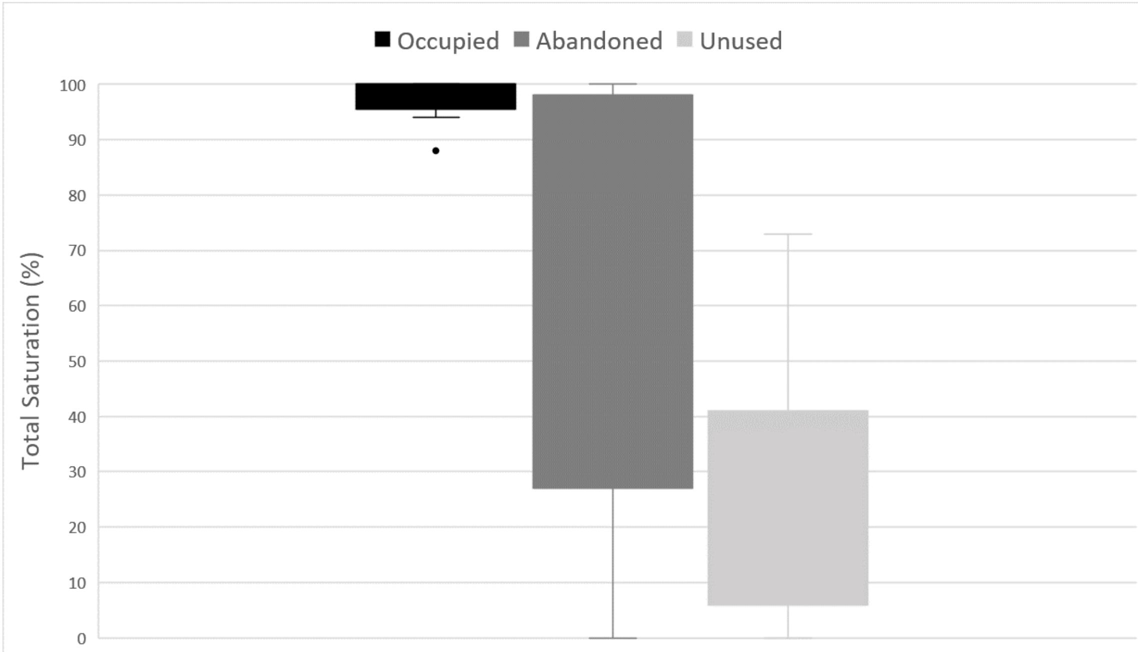

Figure 2.4. Box plot showing total saturation percentage (%) for occupied, abadoned, and unused sites for the Little Truckee River watershed.

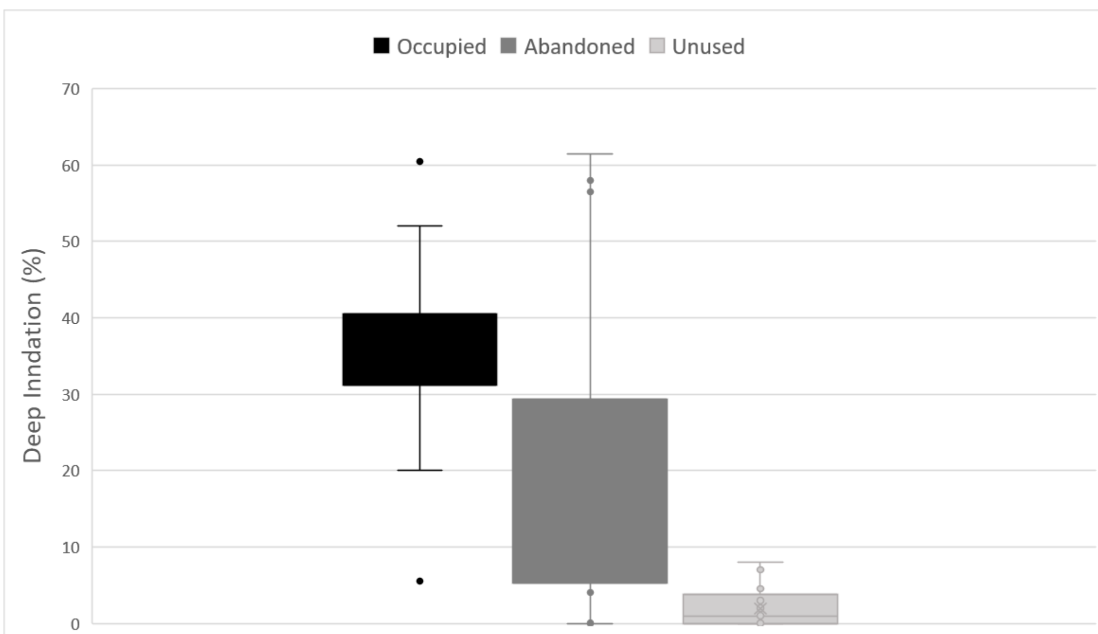

Figure 2.5. Box plot showing deep inundation percentage (%) for occupied, abandoned, and unused sites for the Little Truckee River watershed.

Herbaceous Vegetation Analysis

Herbaceous vegetation varied among the three occupancy types with some dominated by wet emergent species (sedge) and some sites with more mesic and xeric herbaceous vegetation species (grass and forbs) across occupied, abandoned, and unused sites (Figure 2.6). Occupied sites were dominated by sedge herbaceous vegetation at 84% (range = 62% to 95%) followed by grasses at 7%, forbs at 5% and rushes at 4% (Table 2.4). The opposite was true for unused sites, which were dominated by grasses at 35% and forbs at 35% followed by sedges at 26% (range = 0% to 60%) and rushes at 5%. Abandoned sites were mostly dominated by sedges at 65% (range = 7% to 98%) followed by grasses at 17%, forbs at 16% and rushes at 2%. Twelve of the abandoned sites were within the sedge range of 62% to 95%, and five were below this range. Occupied sites had statistically different sedge coverage values when compared to unused sites (Wilcox function and Mann-Whitney statistical test, p-value < 0.02) but were not statistically different than abandoned sites (Figure 2.7).

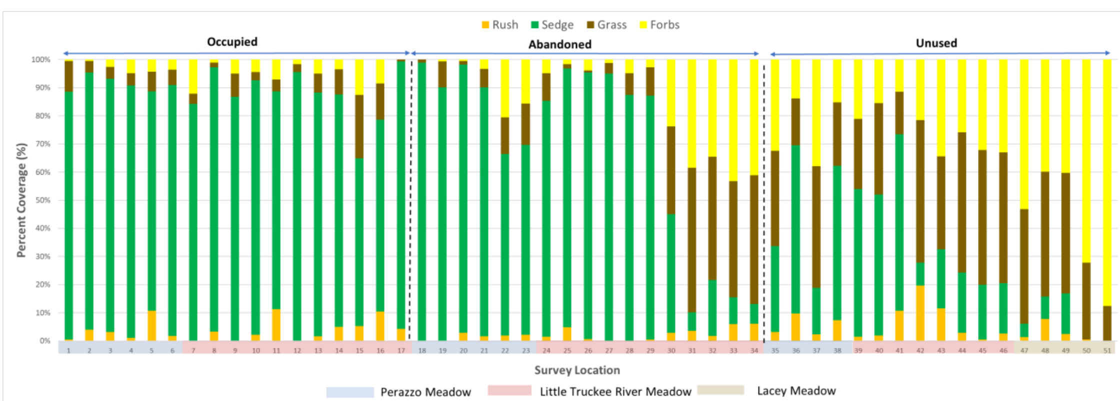

Figure 2.6. Distribution of herbaceous vegetation coverage (%) for occupied, abandoned, and unused sites of the Little Truckee River watershed (n= 51 survey sites).

Table 2.4. Herbaceous vegetation type results for occupied, abandoned, and unused sites for the Little Truckee River watershed.

	Occupied (O)			Abandoned (A)			Unused (U)			*P-Value*		
VARIABLE	Mean	S.D	Range	Mean	S.D	Range	Mean	S.D	Range	O vs. U	O vs. A	U vs. A
Rush %	4	8	(0 - 11)	2	2	(0 - 6)	5	6	(0 - 22)	0.31	0.56	0.07
Sedge %	84	8	(62 - 95)	65	34	(7 - 98)	26	21	(0 - 60)	<.02	0.18	<.02
Grass %	7	5	(1 - 24)	17	17	(1 - 51)	35	13	(13 - 57)	<.02	0.16	<.02
Forbs %	5	4	(0 - 13)	14	16	(0 - 43)	35	20	(11 - 88)	<.02	0.34	<.02

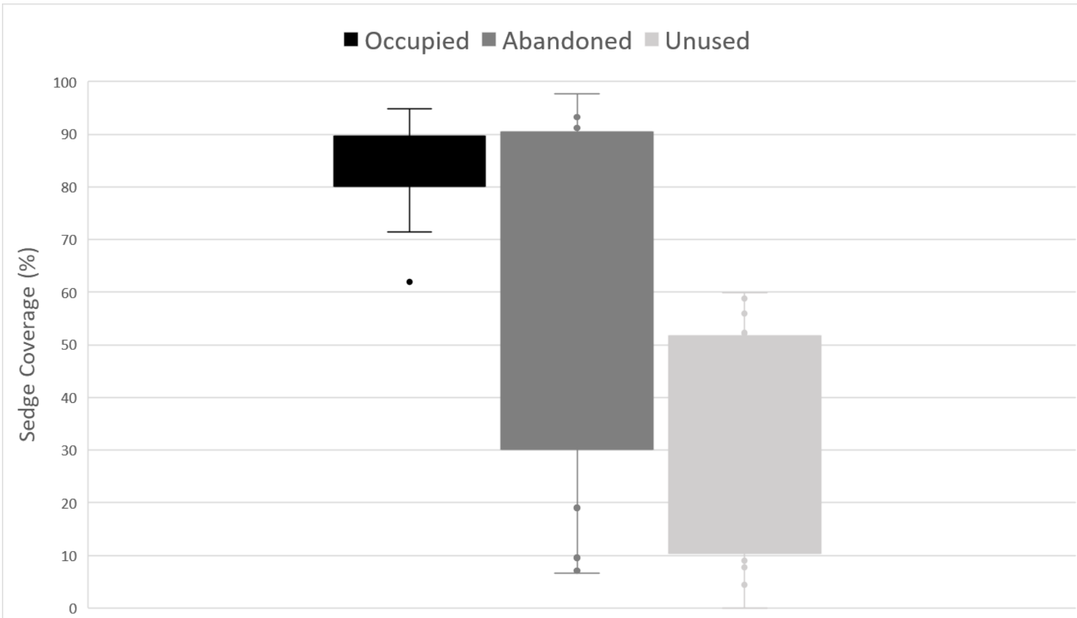

Figure 2.7. Box plot showing sedge coverage for occupied, abandoned, and unused sites for the Little Truckee River watershed.

Food Analysis

Both total food abundance and Willow Flycatcher food abundance were significantly different across occupied, abandoned, and unused sites (Figure 2.8). Occupied sites had the largest total food abundance of 105 food items (range = 30 to 274) and total Willow Flycatcher relative food abundance of 16 food items (range = 7 to 33). Unused sites had a total food abundance of 52 food items (range = 31 to 105) and Willow Flycatcher relative food abundance of 3 food items (range = 0 to 7). Abandoned sites had total food abundance of 95 (range = 21 to 288) and Willow Flycatcher relative food

abundance of 9 (range = 0 to 28). The percent of available food considered to be Willow Flycatcher food varied at the different locations. In occupied sites, 15% of available food was Willow Flycatcher food. In abandoned sites, this value was 9%, and in unused sites, the value was 5%. All three occupancy types had statistically different values for both total food abundance and Willow Flycatcher relative food abundance (p-value < 0.02) (Table 2.5).

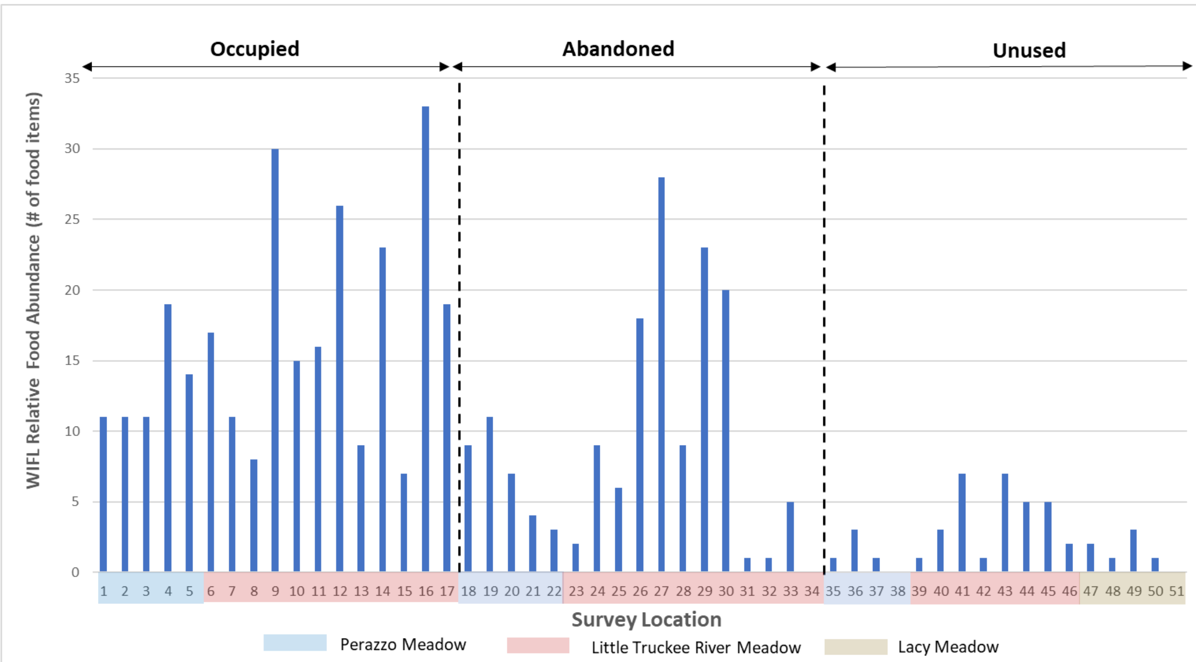

Figure 2.8. Willow Flycatcher relative food abundance for occupied, abandoned, and unused sites for the Little Truckee River watershed (n= 51 survey sites).Willow Flycatcher = WIFL.

Food taxa composition varied across occupied, abandoned, and unused sites (Table 2.5). Of the six taxa that were found within each occupancy type, Diptera and Hemiptera combined to make up more than 80% of the food samples for all sites (occupied 88%, abandoned 93%, unused 82%). Food samples collected in occupied sites

had the highest abundance of Odonata, Araneae, and Diptera, while food samples collected in unused sites had the highest abundance of Hemiptera, Hymenoptera and Coleoptera.

Table 2.5. Food metric results for occupied, abandoned, and unused sites for the Little Truckee River waterhsed.

	Occupied (O)			**Abandoned (A)**			**Unused (U)**			***P-Value***		
VARIABLE	Mean	S.D	Range	Mean	S.D	Range	Mean	S.D	Range	O vs. U	O vs. A	U vs. A
Odonata	4	5	17, (0 - 17)	3	4	14, (0 - 14)	0	1	2, (0 - 2)	0.29	<.02	<.05
Araneida	6	4	13, (1 - 14)	3	3	8, (0 - 8)	3	2	6, (0 - 6)	<.02	<.02	<.02
Hemiptera	18	19	55, (0- 55)	17	22	89, (1 - 90)	22	21	75, (0 - 75)	1	0.66	1
Coleoptera	1	2	5, (0 - 5)	0	0	1, (0 - 1)	2	2	8, (0 - 8)	<.05	0.59	<.02
Hymneoptera	2	1	4, (0 - 4)	1	2	4, (0 - 4)	5	5	19, (0 - 19)	<.02	<.02	<.02
Diptera	79	55	222, (19 - 241)	71	58	180, (4 - 184)	22	11	38, (7 - 45)	0.55	<.02	<.05
Total Abundance	105	65	244, (30 - 274)	95	72	287, (21 - 288)	52	20	74, (31 - 105)	<.02	<.02	<.02
Willow Flycatcher Relative Food Abundance	16	8	26, (7 -33)	9	8	28, (0 - 28)	3	2	7, (0 - 7)	<.02	<.02	<.02

Hydrologic, Herbaceous Vegetation, and Food Relationships

All occupied sites fall within a range of 88% to 100% for total saturation and 62% to 95% for sedge coverage (Figure 2.9). All unused sites have less than 88% total inundation and 62% sedge coverage and thus both hydrologic and vegetation condition do not overlap with those observed for occupied sites. Among the abandoned sites, ten fell within the range for occupied sites for both sedge coverage and total saturation. These sites will be considered further in the discussion. There is a significant positive linear relationship between sedge coverage and total saturation (R^2= 0.91) for all surveyed locations (Figure 2.9). The relationship is not quite one to one (slope= 0.82), because many sites with 90% to 100% total saturation have 65% to 90% sedge coverage. There was no siginificant linear relationship between Willow Flycatcher relative food abundance and total saturation, but 93% of the sites (n=25) within the 88% to 100% range for total saturation had greater than 7 for total Willow Flycatcher relative food abundance (Figure 2.10). Only 13% of the sites (n=3) with less than 88% total saturation and had total Willow Flycatcher relative food abundance value greater than 7.

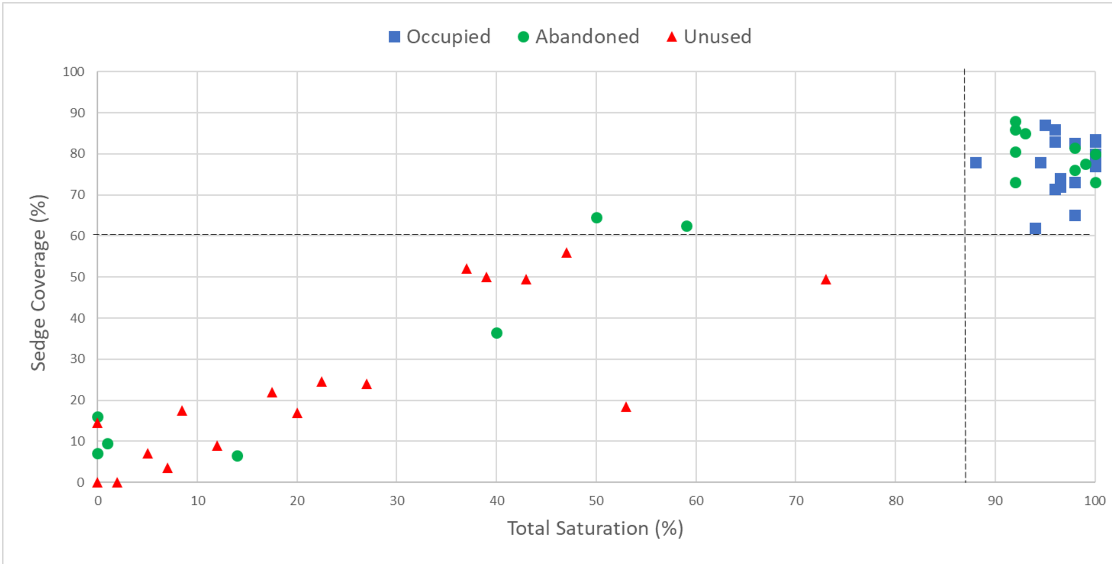

Figure 2.9. Sedge coverage (%) vs. total saturation (%) for occupied, abandoned, and unused sites for the Little Truckee River watershed.

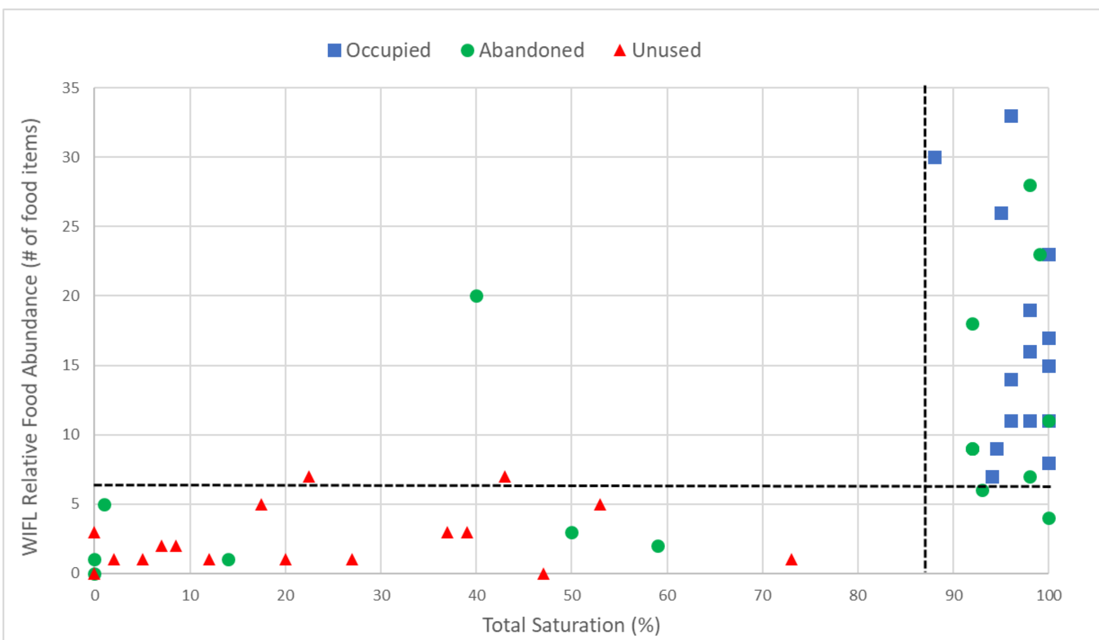

Figure 2.10. Willow Flycatcher relative food abundance vs. total saturation (%) for occupied, abandoned, and unused sites in the Little Truckee River watershed. Willow Flycatcher = WIFL.

DISCUSSION

Hydrologic Conditions

Occupied locations had near fully saturated soil conditions with levels of saturation exceeding 88%. Previous studies of occupied meadows in Little Truckee River watershed found differing saturation conditions in territories. Sanders and Flett (1987) found 40% to 90% standing water in territories, and Bombay et al. (2003) found 44% standing water conditions in territories. The higher total saturation values found in our study are most likely due to the total saturation measurement which took into account not only areas with standing water but also areas that did not have standing water but did have ground that was fully saturated. A more comparable measurement would be deep inundation which varied from 20% to 52% for occupied sites in 2017 and is within the range of total area with standing water found in previous studies.

The saturated soil conditions in territories of our study were similar to territories in Warner Valley of the Sierra Nevada, where we performed the same hydrologic habitat survey in five territories observed in 2019 (total saturation = 94% to 100%). Similar fully saturated soil conditions near nests were also found in an earlier study of territories in Warner Valley (King and King 2003). The near fully saturated soil conditions found in occupied sites hints that occupied sites may be completely inundated early in the season during spring runoff. Areas that were saturated but did not have standing water suggest that some areas may be fully inundated (standing water) early in the summer but not necessarily later in the summer. This finding is similar to Sanders and Flett (1989) who found that a large amount of standing water in territories early in the season but by the end of the breeding season much of the standing water had disappeared.

Near fully saturated soil conditions found in occupied sites were found to be important to Willow Flycatcher habitat but the amount of standing water was also found to be important. Nearly one third of the standing water in occupied locations we surveyed was deep, and half of the deep water had emergent vegetation. Bombay et al. (2003) also found deep standing water to be important in territories with slightly deeper standing water conditions found within active territories compared to areas that were not occupied. The abundance of deep water later in the summer is likely important for sustaining production of aquatic insect taxa such as Odonata and Diptera, which were both important food items for nesting Willow Flycatcher (Chapter 3).

Herbaceous Vegetation Conditions

We found that occupied sites had much more sedge vegetation compared to unused sites. Territories in the Sierra Nevada (Bombay et al. 2003) and Warner Valley in the northern Sierra Neavda (King and King 2003) were also dominated by sedge. We also found that sedge coverage increased with increased total saturation and forb vegetation coverage decteased with an increae in total saturation. This finding is similar to a study in the Sierra Nevada (Bombay et al. 2003) that found wet meadows had fewer forbs than unoccupied meadows that were not as wet. Sedge is thought to be important part of Willow Flycatcher habitat because of the substrate and structure it provides for adult aquatic insects and terrestrial insects that may forage within meadows (Green et al. 2003). This study suggests that 62% to 95% sedge coverage is an optimal range for sites that are occupied by Willow Flycatcher.

Food Abundance

We found both total food abundance and Willow Flycatcher food abundance to be highest within occupied sites, which also were exclusively saturated at levels greater than 88%. Increased wetness corresponds with increased food abundance (Serena 1982, Green et al. 2003). In a study of Southwestern Willow Flycatcher diet in Nevada and Arizona, Wiesenborn and Heybon (2007) found that Willow Flycatcher diets varied with the amount and type of water present. They found higher numbers of Odonata taxa within Willow Flycatcher diets in territories with a large amount of pond habitat features. These findings indicate that not only is the level of inundation or saturation important but also the type of standing water may be important (deep vs. shallow and slow vs. fast) to food production dynamics within meadows.

Abandoned Sites

Abandoned sites were no longer occupied for two different reasons. Seven of the seventeen abadoned sites had smaller percent coverage of total saturation, sedge, and Willow Flycatcher relative food abundance than found in any occupied site. Ten of the seventeen abandoned sites had total saturation and sedge vegetation levels that were within the range observed for occupied sites. In all of these 10 cases, comparison of field observations in 2017 with historical aerial photos indicate that willow shrub quality had previously satisfied flycather requirements but had declined in recent years, no longer meeting shrub standards for occupied territories. The ten abandoned sites were within areas that had been previously restored by a plug-and-pond approach which substantially increased water levels. The observed decline in willow shrub coverage and foliar density is consistent with high water levels stressing or killing willow shrubs, such as seen after

beaver dams are built. We attribute the abandonment of these sites to the absence of suitable willow shrub habitat.

Habitat Requirements

Our study provides evidence that Willow Flycatcher nesting habitat in the Sierra Nevada can be characterized by three essential elements: extensive water saturation, adequate willow shrubs, and sedge vegetation. In meadows of the Little Truckee River watershed, willow shrubs function as nesting, foraging, and singing structures and the willow shrub requirements previously defined by Bombay et al. (2003) are appropriate for observed occupied sites in this study. Sedge vegetation provides feeding structure for aquatic and terrestrial food items foraged on by Willow Flycatcher. Both deep and shallow unundation provide nurseries for important aquatic food items and may act as a barrier to terrestrial predators. The three habitat elements are strongly interrelated. Water level must be sufficiently high to establish and maintain willow shrub and sedge and to keep terrestrial vegetation, such as lodgepole pine and sagebrush, from encroaching into the meadow. If water levels are too high, willow shrub quality can decline, no longer providing appropriate habitat for flycatcher occupation. When combined with the existing standards for willow shrub coverage and foliar density, the observed range of total saturation, deep inundation, and sedge coverage for occupied sites exclusively define the necessary habitat for Willow Flycatcher within the Little Truckee River watershed (Table 2.6). These habitat reference ranges can be used to guide management and restoration actions when attempting to restore or maintain optimal Willow Flycatcher habitat conditons in meadows of the Sierra Nevada.

Table 2.6. Willow Flycatcher preferred habitat requirements.

Habitat Requirement	Water	Shrubs	Herbaceous Vegetation
Metric	Total Saturation, Deep Inundation	Foliar Density, Shrub Coverage	Sedge Coverage
Range (%)	88-100, 20-52	20-60, 35-75	62-95

Habitat Fluctuations

Understanding how the three essential habitat elements can change when meadows are degraded or restored is important for those tasked with managing existing habitat and restoring degraded meadows. Changes in meadow hydrology, whether drying through river channel incision or rewetting during meadow restoration, can have negative impact on flycatcher habitat. The meadow can be either too dry or too wet. Unused sites in this study have adequate willow shrub coverge but are too dry to support adequate sedge vegetation and Willow Flycatcher food production. Abandoned sites either had adequate willow coverage but are too dry (similar to unused sites) or are adequately wet, but did not meet willow shrub requirements because of elevated water levels impacting willow shrub density and health.

The combination of saturation, sedge, and willow shrubs required for flycatcher habitat is illustrated for a schematic abandoned channel meander (oxbow) in Figure 2.11. Successful habitat combines extensive saturation and inundation, including both deep and shallow standing water, with adequate and vigorous shrub coverage, and extensive sedge coverage. Sedge is absent in deeper parts of the oxbow channel but abundant in the shallower inner portion of the channel and point bar. Inner portions of the abandoned oxbow allow establishment of shrubs with adequate coverage and spacing. The area is flooded early in the year and the floodplain is well connected to the main stream channel in the meadow.

If stream incision has occurred, the meadow is less frequently and deeply flooded, causing it to dry out more quickly and leading to dense stands of willow shrubs within the abandoned oxbow channel. Sedge vegetation on the inner bar of the oxbow is no longer saturated and is replaced by grass and forbs. The abundance of aquatic food resources decreases with the reduction in standing water and foraging opportunites are limited within the dense shrubs established in the former channel. Channel and meadow restoration can provide increased flooding and longer inundation periods and a transition back to sedge, providing conditions found in the predisturbed or natural state. However, high water levels can lead to an initial decrease in shrub quality, particularly within the abandoned oxbow channel, causing shrub conditions to no longer be suitable for nesting. An example of this is seen in abandoned sites where “pond and plug” restoration causes increased inundation and a decrease in shrub quality. Adequate shrub conditions may reestablish on the channel banks, although many years to decades are required to achieve the size and coverage needed to meet shrub requirements.

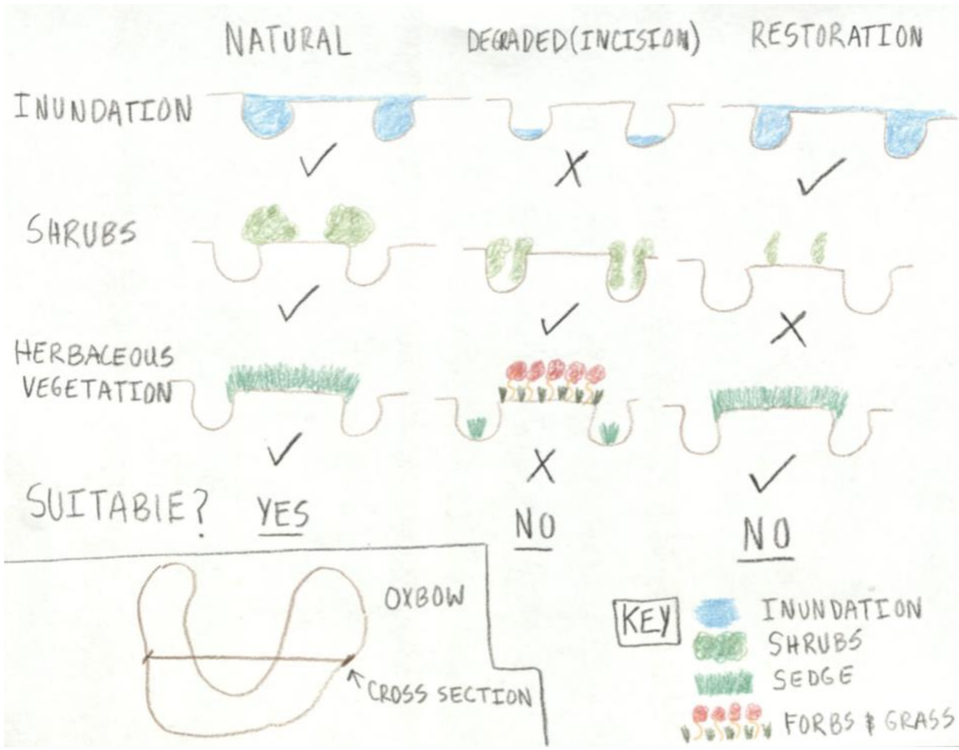

Figure 2.11. Willow Flycatcher habitat suitability differences for different meadow channel conditions (natural, degraded, restored). Habitat suitability dependent upon thresholds for habitat requirements (saturation and inundation, shrubs, sedge vegetation).

CONCLUSION

We identified 17 WIFL territories in 2017 in the Little Truckee River watershed. We measured hydrologic, herbaceous vegetation, and food conditions in each occupied site and compared these conditions to those in 17 territories identified in earlier surveys (1997-2010) that were no longer occupied in 2017. We also evaluated habitat in 17 sites, termed unused sites, with adequate willow shrub habitat but where no Willow Flycatcher nesting has been observed. Occupied sites had at least 88% total saturation, with 20% to 52% of the site inundated deeper than six inches. Occupied sites also had sedge coverage between 62% and 95%. Greater abundance overall of arthropod food items, including those items favored by Willow Flycatcher, was found in occupied sites, consistent with

their wetter condition. Unused sites and seven of 17 abandoned sites were dryer, with total saturation and sedge coverage smaller than that observed for occupied sites. Ten of the 17 abandoned sites had total saturation and sedge coverage consistent with the occupied sites, but the condition of the willow shrubs was found to be degraded because of high water levels associated with recent pond-and-plug restoration. These abandoned territories may recover, but only after new willow growth provides the coverage and density required for Willow Flycatcher habitat.

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CHAPTER III

DIET AND FORAGING BEHAVIOR OF BREEDING WILLOW FLYCATCHER IN SIERRA NEVADA MEADOWS

INTRODUCTION

Habitat requirements for Willow Flycatcher in Sierra Nevada meadows has largely been established based on habitat conditions observed in meadows occupied by Willow Flycatcher (Serena 1982, Sanders and Flett 1989, Bombay et al 2003). Although these studies have increased our general knowledge of Willow Flycatcher habitat, it would be useful to establish food/habitat relationships that can help explain why certain habitat features are needed within meadows. For example, water has long been thought to be important feature in meadows occupied by Willow Flycatcher (Serena 1982, Sanders and Flett 1989, Green et al. 2003), but little ecological evidence exists to demonstrate the need for water within Sierra Nevada meadows. Specific information on food production benefits of aquatic habitat features such as streams and ponds could be used to better manage existing habitat and restore food production and foraging opportunities in degraded meadow systems.

Food/habitat relationships within meadows require an understanding of diet and foraging behavior. In the absence of specific information on Willow Flycatcher diet in Sierra meadows, Willow Flycatcher diets and foraging behavior in Sierra meadows has been presumed to be similar to that for flycatcher outside of the Sierra Nevada (Green et al. 2003). Willow Flycatcher diet and foraging may be opportunistic and could well differ in Sierra meadows compared to non-meadow habitat often associated with Southwestern subspecies (*E. t. extimus*). Studies into Willow Flycatcher diet and foraging behavior are

needed in order to gain a broader understanding of food/habitat relationships in Sierra Nevada meadows and to determine whether meadows are producing enough food for nesting Willow Flycatcher.

In this study, I use direct observation of Willow Flycatcher foraging along with video footage of nestlings being fed to evaluate Willow Flycatcher diets and foraging behavior. Continuous filming throughout the day allowed for an assessment of diurnal diet and foraging patterns that can give further insight into food/habitat relationships and inform overall diet and foraging behavior within Sierra meadows.

To better understand the overall diet and foraging behavior of Willow Flycatcher in Sierra Nevada meadows, this study was organized around four main questions: (1) What are the important food taxa and food items of Sierra Nevada meadow diets? (2) How does Willow Flycatcher diet in Sierra Nevada meadows differ from diets in non-meadow habitat? (3) Is aquatic habitat important for food production within Sierra Nevada meadows? (4) Do different foraging strategies exist within Sierra Nevada meadows?

STUDY AREA

One of the largest remaining populations of breeding Willow Flycatcher in the Sierra Nevada is found in the Little Truckee River watershed and surrounding area (Serena 1982, Green et al. 2003, Mathewson et al. 2013), located approximately 20 miles north of Lake Tahoe, California in the Sierra Nevada Mountain Range (Figure 3.1). Six active Willow Flycatcher nests were identified and filmed in the summer of 2018. Four nests were located in meadows within the Little Truckee River watershed and two nests were located in a meadow in the nearby Yuba River watershed.

The four nests in the Little Truckee River watershed are in the Little Truckee River Meadow, Perazzo Meadow, and Stampede Meadow (Figure 3.1). Both Perazzo and Little Truckee River meadows are located within large river valleys with flat valley bottoms dominated by patches of willow shrubs (*Salix* sp.) and emergent herbaceous vegetation (*Carex* sp.). Perazzo Meadow has an anastomosing stream channel with multiple small abandoned meandering channels (oxbows). Little Truckee River Meadow has an active single thread meandering stream channel that includes historic and active floodplain features (point bar, abandoned flood channels, and oxbows). Pond-and-plug restoration projects in both Perazzo Meadow (2010) and Little Truckee River Meadow (2012) transformed much of the landscape and both meadows are currently in a state of recovery with large ponds evident throughout both meadows. Stampede Meadow is a delta meadow, formed where the Little Truckee River enters Stampede Reservoir downstream of both Perazzo and Little Truckee River meadows. Stampede Meadow is dryer than the other two meadows and is dominated by a grass/forb herbaceous vegetation and includes a nearby riparian corridor composed of willow, cottonwood, and aspen trees.

The fourth meadow surveyed was Milton Meadow in the Yuba River watershed where the Middle Fork of the Yuba River enters Milton Reservoir 11 miles northwest of the Perazzo and Little Truckee River meadows (Figure 3.1). Milton Meadow is within a large, high elevation delta complex between two large distributary channels along the lower part of the delta. The vegetation within Milton Meadow is similar to that of Perazzo and Little Truckee River meadows with the exception of larger willow shrubs and the presence of large cottonwood trees and alder shrubs (*Alnus* sp.). Milton Meadow

also has an extensive stream channel network characterized by medium and fast flowing water.

Four Willow Flycatcher subspecies are recognized in North America but only three are found in the western portion of the United States (Unitt 1987). The Little Truckee River watershed area is north of the range of Southwestern Willow Flycatcher (*E. t. extimus*) and therefore the possible subspecies are *E. t. adastus* and *E. t. brewsteri*. Throughout this paper, the term Willow Flycatcher will be used to represent both *E. t. adastus* and *E. t. brewsteri* because distinguishing between the two sub species is difficult and both can inhabit the study area.

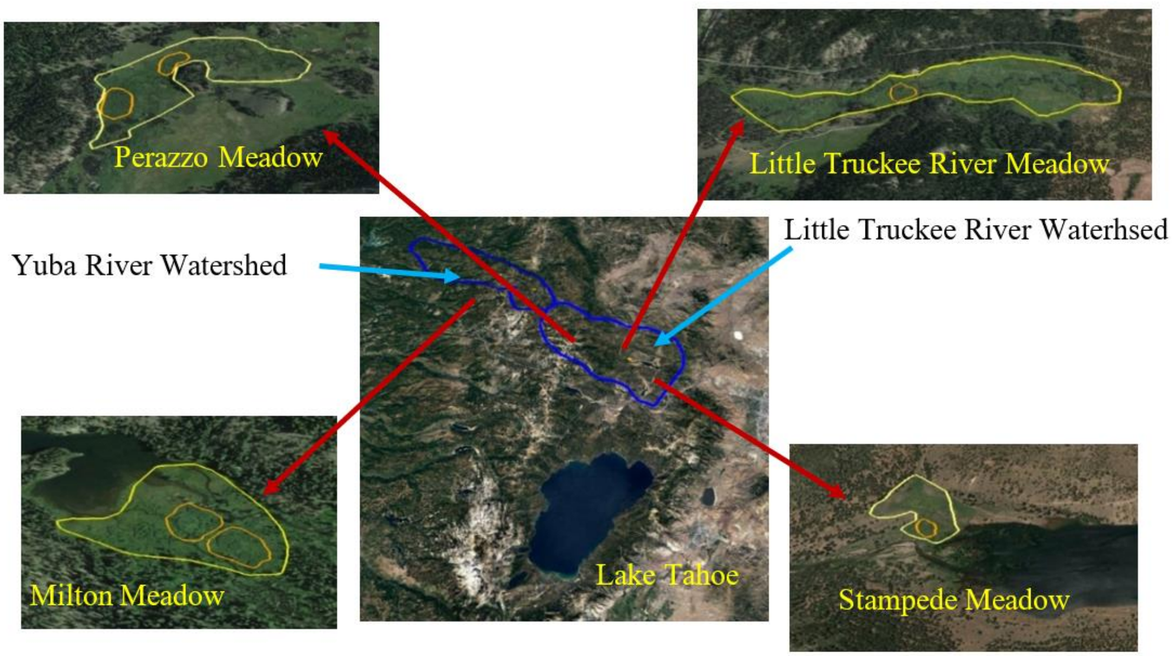

Figure 3.1. Little Truckee River Study area, watershed (blue), meadow (yellow) and territories (orange). Photo Credit, Google Earth.

METHODS

I used a high resolution, tripod-mounted video camera to film nests as adults brought food items to nestlings within each territory. The video camera was positioned at a distance of 3 to 5 meters (9-15 ft) from the nest with a clear view of the nestlings. I was careful to minimize unwanted stress to nestlings and adults as they attended to the nest. If the camera appeared to be causing abnormal or stressed behavior, it was repositioned farther from the nest or removed and replaced at a later time. Filming duration varied for each nest site, but all nests were filmed for a minimum of 8 hours (Table 3.1). Diurnal variation in foraging and feeding was evaluated at two sites, PERR-6 and MILTON-1, for which continuous video through a single day was possible and the video record was most complete. For each site, video footage of nestlings feeding was examined using slow motion video software to identify individual food items that were delivered to nestlings. It was possible to identify the majority of food items delivered to nestlings, although 20% of food items could not be identified due to feeding pace, nest obstructions, or video blur. Only food items that could be confidently identified were included in the diet analysis.

I observed Willow Flycatcher as they foraged and returned to feed nestlings, recording foraging location (inside territory vs. outside of territory), foraging method (gleaning vs. hawking), habitat used (water, willow shrub, grass/forbs, conifer forest), and time of feeding. The combination of foraging observations and video footage allowed food items to be linked to foraging location, foraging method, and foraging habitat. Boundaries for each of the six territories were determined by identifying were male adults were singing and actively defending at a site. A territory polygon was drawn based on previous singing and territorial locations so that territory boundaries could later be

identified. Observations within PERR-6 and MILTON-1 were divided into four different time periods so that diurnal patterns could be identified: morning (6:00-10:00), midday (10:00-14:00), late day (14:00-18:00), evening (18:00-21:00).

Table 3.1. The duration of video footage (hrs) for each territory and time period.

Territory	**Morning (hrs)**	**Midday (hrs)**	**Late day (hrs)**	**Evening (hrs)**	**Total (hrs)**
PERR-6	12.5	14.5	12	7	46
PERR-1	0	2	4	2	8
MILTON-1	3	7.5	6.5	3	20
MILTON-2	0	4	4	2.5	11
STAMPEDE-1	0	4	4	2.5	11
LT-3	0	2	4	2	8
Total (hrs)	**15.5**	**34**	**34.5**	**19**	**103**

RESULTS

Diet: Composition and Occurrence

Of the 104 hours of video footage, I was able to identify 1,298 (80%) food items out of a total of 1,640 food items delivered to nestlings. Ten major food taxa (orders) were represented in the Willow Flycatcher diet across the four meadows and six territories. Lepidoptera (19%) and Raphidioptera (19%) were the most abundant food taxa, followed by Hemiptera (13%), Odonata (12%), and Ephemeroptera (12%) (Table 3.2, Figure 3.2). The remainder of the diet was largely composed of Diptera (11%) and Hymenoptera (9%), with less abundant food taxa such as Coleoptera (3%), Orthoptera (2%), and Plecoptera (1%). A majority of the food taxa were dominated by one food item: deerfly (Diptera), leaf hopper (Hemiptera), moth caterpillar (Lepidoptera), snakefly (Raphidioptera), ladybug beetle (Coleoptera), and wasp (Hymenoptera).

Of the ten food taxa found in the diet Odonata, Hymenoptera, Diptera, and Lepidoptera had the highest percent occurrence (Table 3.2). Hemiptera and

Ephemeroptera were the next most common, being found in four diets, and Coleoptera and Plecoptera were present in half of the diets. Raphidioptera and Orthoptera were the least common food taxa and only found within two diets.

Composition and food item abundance varied across meadows. Perazzo Meadow was dominated by five major food taxa (Raphidioptera, Lepidoptera, Hemiptera, Odonata, and Diptera) and had a high percent composition of Raphidioptera and Diptera (Figure 3.3, Figure 3.4). The territories within Perazzo Meadow also differed, PERR-6 was the only territory with Raphidioptera and had a higher percent composition of Hemiptera than PERR-1, whereas PERR-1 had a higher percent composition of Lepidoptera and Diptera. Milton Meadow was dominated by four food taxa (Ephemeroptera, Lepidoptera, Hemiptera, and Hymenoptera) and had the highest percent composition of Ephemeroptera and Coleoptera. Both territories within Milton Meadow were similar but MILTON-2 did not have any Raphidioptera and had a lower percent composition of Ephemeroptera. Stampede Meadow was dominated by Orthoptera, Odonata, Lepidoptera, and Hymenoptera and was the only meadow with a significant abundance of Orthoptera and had the highest percent composition of Hymenoptera of all the meadows. Little Truckee River Meadow had the highest percent occurrence of Odonata and Lepidoptera of all the meadows and was the only meadow that was dominated by both taxa. LTR-3 was also the only territory where Plecoptera were targeted and made up a significant portion of the diet.

Figure 3.2. Willow Flycatcher feeding moth caterpillar (left) and mayfly (right) to nestlings.

Table 3.2. Willow Flycatcher diet abundance, composition, and occurrence data.

Taxon (order)	Abundance (individuals)	Percent Composition (%)	Taxon (order)	Percent Occurrence (% (n=6))
Lepidoptera	250	19.3	Lepidoptera	100 (6)
Raphidioptera	246	19.0	Odonata	100 (6)
Hemiptera	165	12.7	Diptera	100 (6)
Odonata	160	12.3	Hymenoptera	100 (6)
Ephemeroptera	160	12.3	Hemiptera	66 (4)
Diptera	138	10.6	Ephemeroptera	66 (4)
Hymenoptera	113	8.7	Coleoptera	50 (3)
Coleoptera	32	2.5	Plecoptera	50 (3)
Orthoptera	21	1.6	Raphidioptera	33 (2)
Plecoptera	13	1.0	Orthoptera	33 (2)

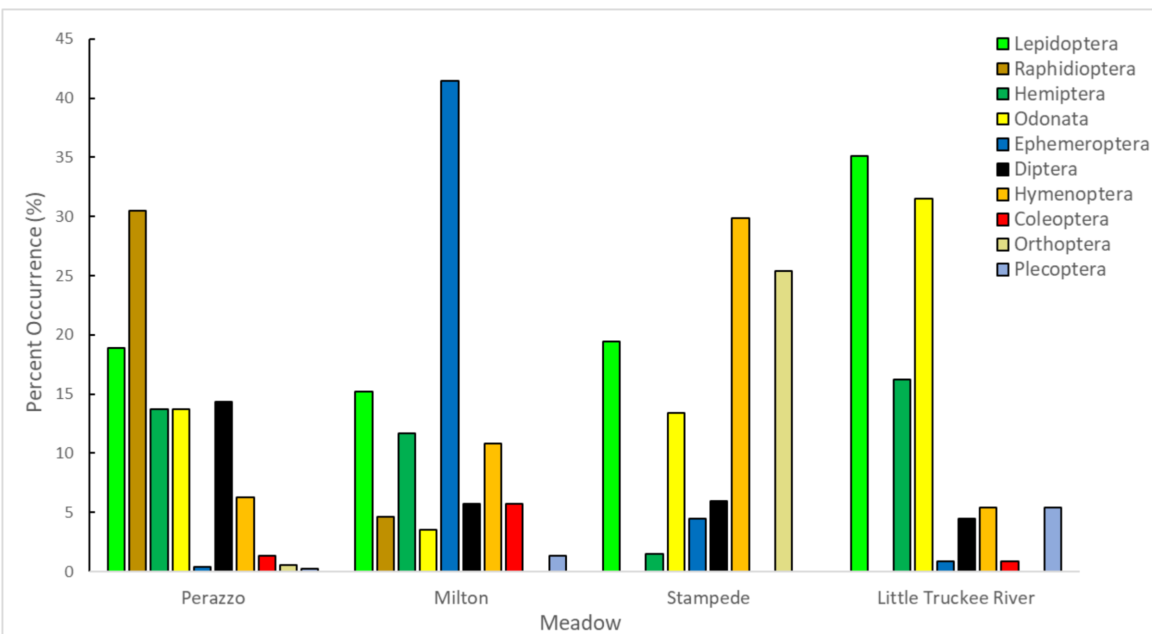

Figure 3.3. Percent composition (%) of food taxa (order) for each meadow.

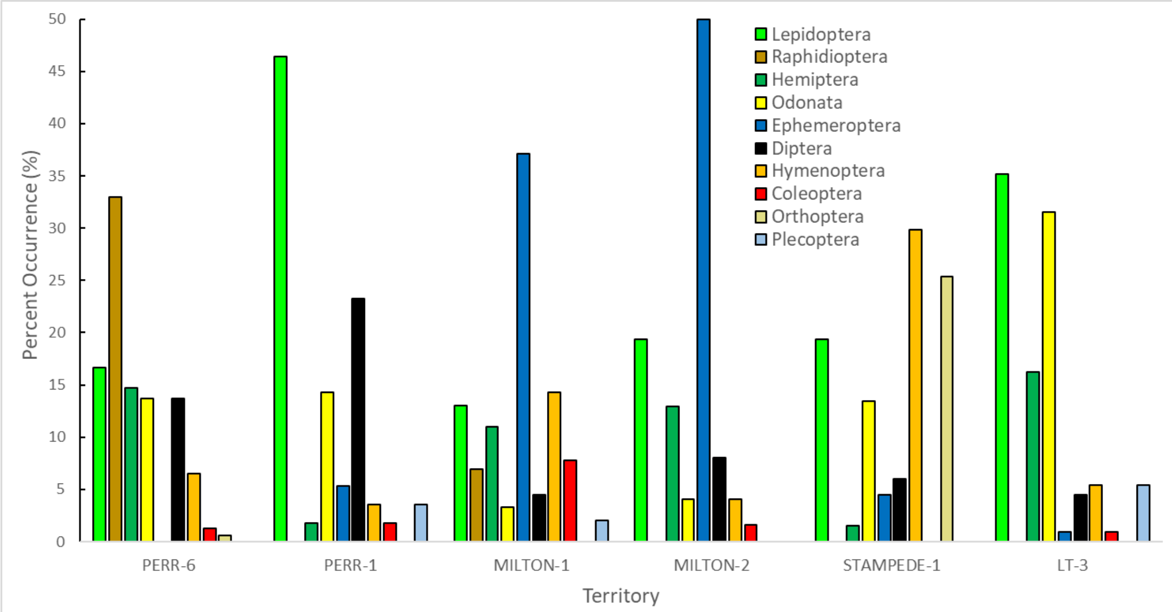

Figure 3.4. Percent composition (%) of food taxa (order) for each territory.

Food/Habitat Relationships

Willow Flycatcher forage in meadows from a range of habitats and habitat features (water, shrubs, grass/forbs, forest). In order to understand which habitat and habitat features are most important for producing the desired food items, I assigned each food item to one of the four habitat or habitat features based on literature (Erman 1984) and field observations. I then used food item percent compositions to determine the percentage of each habitat or habitat feature in the overall diet and individual territory diets. Deerfly, mayfly, stonefly, damselfly, and dragonfly were associated with water habitat and composed 37% of the overall diet, ranging from 24% (STAMPEDE-1) to 62% (MILTON-2) (Figure 3.5). Moth caterpillar, wasp, and leaf hopper were associated with willow shrubs and composed 41% of the overall diet, ranging from 36% (MILTON-2) to 57% (LT-3). Forest habitat composed 19% of the overall diet and were represented entirely by snakefly in the MILTON-1 (7%) and PERR-6 (33%) territories. Ladybug

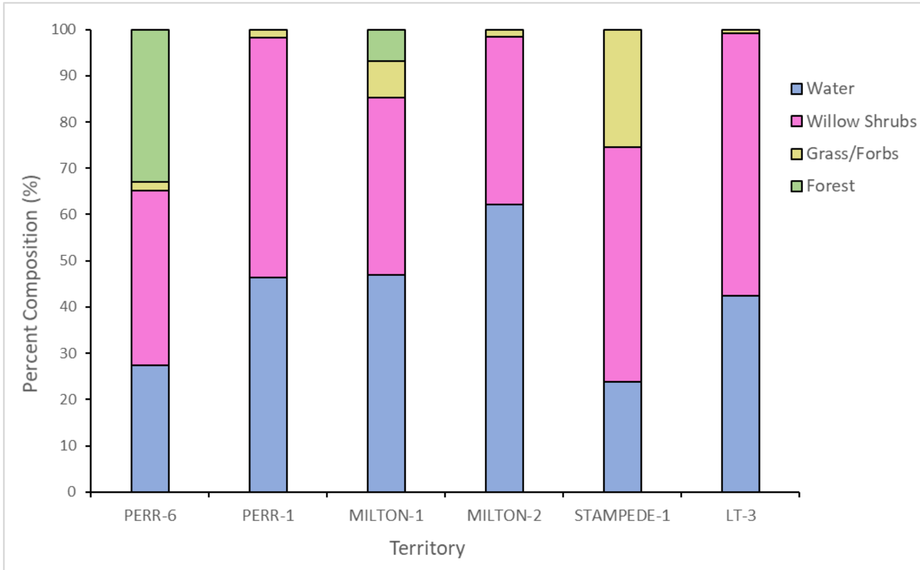

Figure 3.5. Habitat and habitat feature percent composition (%) for each territory.

beetles and grasshopper were associated with grass/forbs vegetation and composed 3% of the overall diet, ranging from LT-3 (1%) and STAMPEDE-1 (25%).

Foraging Behavior

Willow Flycatcher typically use two foraging methods to capture food items: gleaning (catching food by hovering over vegetation or ground) and hawking (catching food through the air) (Fitzpatrick 1980). In order to better understand Willow Flycatcher foraging, I assigned each food item to a foraging method based on field observations and general understanding of food capture tendacies. Snakefly, leaf hopper, grasshopper, ladybug beetles, and moth caterpillar were caught most often by gleaning, whereas mayfly, stonefly, deerfly, wasp, damselfly, and dragonfly were more often caught by hawking. Based on the percent occurrence of each food item and its associated dominant foraging method, 49% of the food items were obtained by gleaning and 51% by hawking. Although, overall hawking and gleaning percent frequency was nearly equal, foraging

method use did vary across meadows. Milton Meadow and its territories had the highest use of hawking and Perazzo Meadow had the highest use of gleaning, whereas Stampede and Little Truckee River meadows used both methods equally (Figure 3.6).

To develop a better understanding of the domain of Willow Flycatcher foraging, we can compare the percent frquency of food items foraged within and outside of each territory. Each food item was associated with a foraging location either within the territory, outside of the territory but within the meadow, or outside of territory and outside of the meadow. Field observations of Willow Flycatcher foraging were used along with the time of nestling feeding to link food items with a foraging location. Deerfly, damselfly, dragonfly, wasp, leaf hopper, ladybug beetle, and grasshopper were typically associated with habitat within the territory, whereas mayfly and stonefly were associated with habitat found outside of the territory but within the meadow. Snakefly were exclusively associated with forest habitat found outside of the meadow. Overall, 74% of food items were associated with habtiat within the territory, with a range of 49% (MILTON-2) to 96% (STAMPEDE-1) (Figure 3.6). Food items associated with habitat outside of the territory were found in all six territories, but foraging outside of the meadow only occured at PERR-6 (33%) and MILTON-1 (7%).

Diurnal Variation in Diet and Foraging Behavior

Video coverage throughout the day at PERR-6 and MILTON-1 allowed for an investigation into diurnal diet and foraging behavior. Food item percent composition was determined for each four hour period of the day (morning, midday, late day, evening) at PERR-6 and MILTON-1 and later used to determine diurnal trends in foraging location.

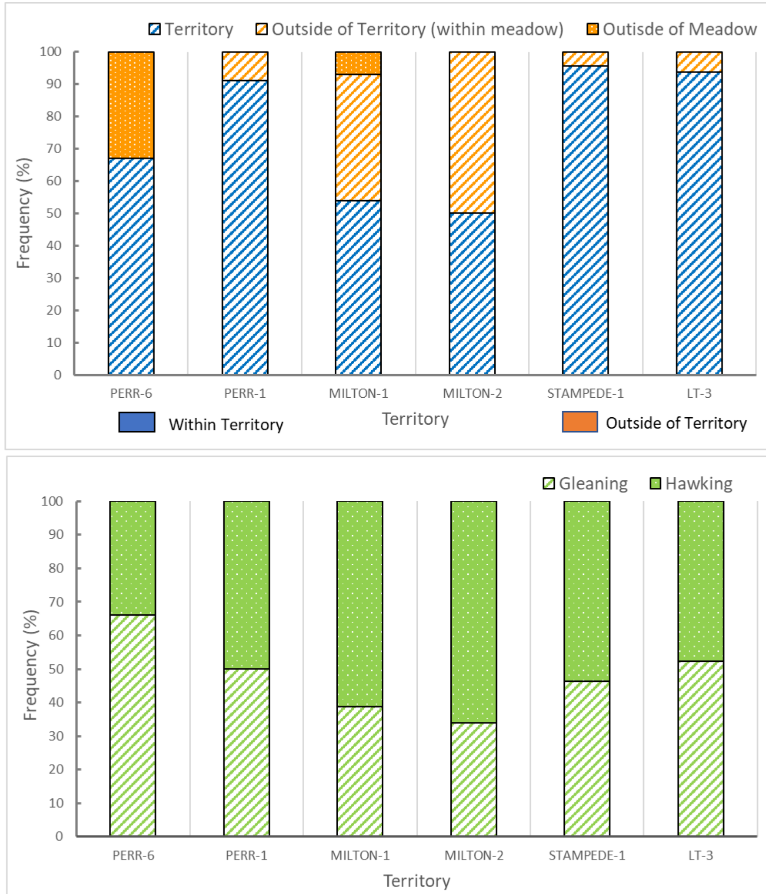

Figure 3.6. Percent frequency (%) of time for foraging location (top) and for foraging method (bottom) for each territory.

The PERR-6 diet was dominated by snakefly (Raphidioptera) and deerfly (Diptera) in the morning but by midday, both moth caterpillar (Lepidoptera) and leaf hopper (Hemiptera) had become the most abundant food items and snakefly largely disappeared from the diet (Figure 3.7). By late day, snakefly once again were abundant and, along with moth caterpillar, was the most abundant food item. Snakefly abundance continued to increase into the evening and, along with damselfly and dragonfly (Odonata), was the most abundant. Although damselfly and dragonfly were never the most abundant food items during any one time period, they were the second or third most abundant over the course of the day.

MILTON-1 was similar to PERR-6 in the morning with a high abundance of snakefly, but wasp (Hymenoptera), rather than deerfly, was the second most abundant food item (Figure 3.7). Similar to PERR-6, the midday diet had an abundance of moth caterpillar and leafhopper whereas snakefly largely disappeared from the diet. By late day, mayfly became the most abundant food item and both moth caterpillar and leaf hopper continued to be abundant. Mayfly were the most abundant in the evening and all other food items were largely absent.

Analysis of the diurnal diet at PERR-6 and MILTON-1 revealed some intriguing diurnal trends. Snakefly and mayfly were typically most abundant in the morning and evening (Figure 3.8). Moth larvae and leaf hopper were usually abundant only in the middle part of the day (midday and late day). Deerfly were typically more abundant in the morning, whereas wasp, damselfly, and dragonfly did not show any strong diurnal trends and were often moderately abundant throughout the day.

Within both territories, Willow Flycatcher tended to forage more often outside of the territory in the morning and evening (Figure 3.9). Both territories showed a peak in foraging within the territory during the midday while foraging outside of the territory often peaked during the evening. Feeding rate was calculated for PERR-6 and revealed that the feeding rate was highest in the morning and evening and lowest in the middle part of the day.

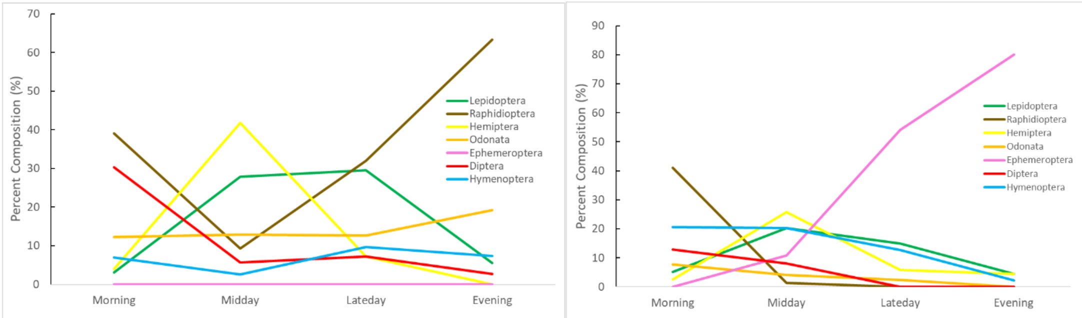

Figure 3.7. Food item percent abundance (%) for the top seven food taxa in PERR-6 (left) and MILTON-1 (right) during each time period.

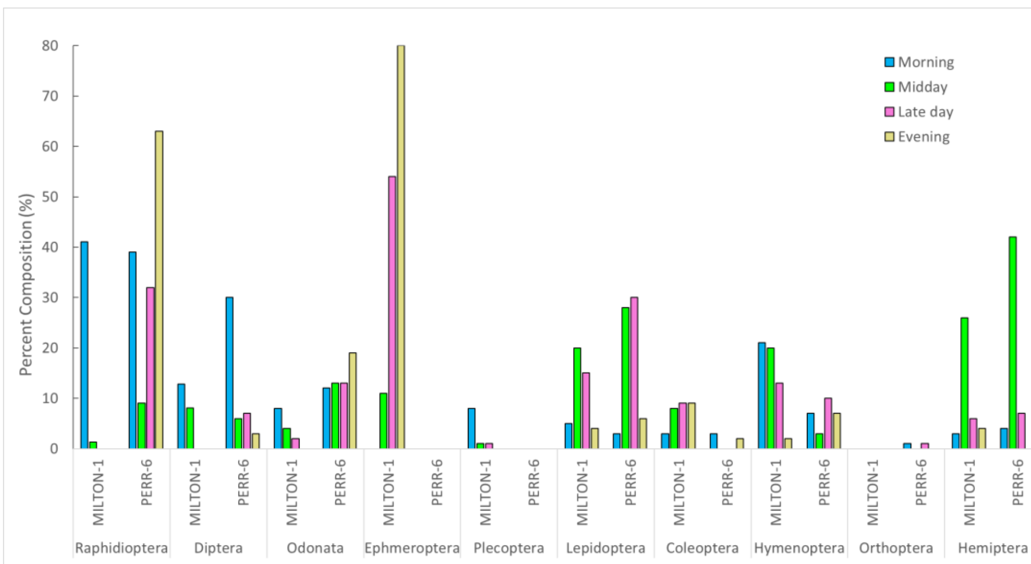

Figure 3.8. Food item percent composition (%) for PERR-6 and MILTON-1 during each time period.

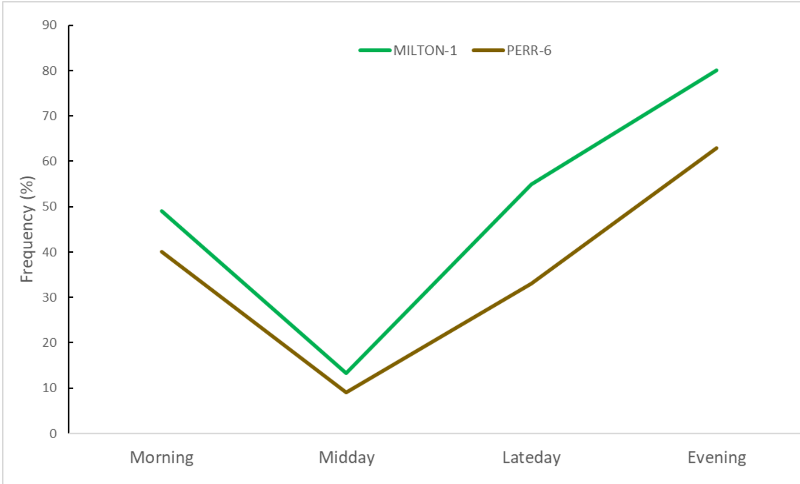

Figure 3.9. Percent frequency (%) of foraging outside of the territory in PERR-6 and MILTON-1 during each time period.

DISSCUSION

Diet

Diet Composition and Food Item Occurrence

Although 75% of the diet was composed of five food taxa, food items were not equally distributed, and some food items were found only in a limited number of meadows and territories. Raphidioptera and Ephemeroptera were largely limited to Perazzo and Milton meadows where habitat conditions were more favorable. It is likely that only meadows with conifer forest nearby can support Raphidioptera foraging and streams suitable for aquatic insect hatches can support Ephemeroptera food items. In contrast, some food taxa such as Lepidoptera and Odonata were not only abundant but had a high percent occurrence in all cases, suggesting they may be more important to Willow Flycatcher across a variety of meadow habitat conditions. Hemiptera, represented by leaf hopper, had a high overall abundance but were not found consistently within all territories and may require specific habitat conditions.

Both Diptera and Hymenoptera, thought to be the most important food items in the Willow Flycatcher diet (Green et al. 2003), had a high percent occurrence but were not as abundant as other food items. Both food taxa are also thought to be represented by a diverse assortment of food items such as deerfly, bees, sawfly, wasp, and ants in the Sierra Nevada (Green et al. 2003), but only deerfly and wasp were found in diets of this study, suggesting that they might not be essential diet in Sierra meadows.

Orthoptera (grasshopper), Coleoptera (ladybug beetles), and Plecoptera (stonefly) were not as abundant as other food items but may be important in meadows where appropriate habitat exist. Grasshopper were largely associated with grass/forbs habitat in STAMPEDE-1, stonefly in stream habitat found near LTR-3, and ladybug beetles in sedge vegetation within MILTON-1.

Sierra Nevada Meadow Diet

The Willow Flycatcher territories examined in this study represent diverse settings, allowing for some generalization of the Willow Flycatcher diet. All Sierra meadow diets, no matter the habitat conditions, appear to have a high abundance of moth caterpillar, with a base of at least 15% to 20% percent composition and some meadows having a higher percent composition. A base food group common to all meadows consists of deerfly (Diptera), wasp (Hymenoptera), leaf hopper (Hemiptera), damselfly (Odonata), and dragonfly (Odonata) and may represent roughly 40% of the diet in Sierra meadows. This base food group along with moth caterpillar can compose more than 75% of the flycatcher diet in some Sierra meadows, as was the case in Little Truckee River Meadow of this study. In each meadow, moth caterpillar and the base food group were supplemented with another food item, including mayfly (Ephemeroptera), snakefly

(Raphidioptera), caddisfly (Trichoptera), or grasshopper (Orthoptera), where these items were abundant. Other food items such as ladybug beetles (Coleoptera) and stonefly (Plecoptera), were present in the Willow Flycatcher diet but made up only a small portion of the diet (0% to 5%).

Are Sierra Nevada Meadow diets different than non-meadow diets?

It is apparent that Willow Flycatcher diets found in Sierra Nevada meadows are different from diets found in non-meadow habitat. We observe aquatic food items to be much more important in meadows compared to non-meadow habitat where aquatic hatch food items are not often found or typically have a low percent composition (Beal 1912, Drost et al. 2007, Durst et al. 2008). Although Hymenoptera and Diptera are common in meadow diets, they make up a smaller percent of the overall diet compared to non-meadow diets (Beal 1912, Drost et al. 2007, Durst et al. 2008). Moth caterpillar are much more important in meadows diets in the Sierra Nevada compared to non-meadow diets where moth caterpillar is either absent (Drost et al. 2003, Durst et al. 2007) or makes up only a moderate portion of the diet (Beal 1912). There are no previous records of snakefly being in flycatcher diets in their breeding range (Green et al. 2003). It is likely that snakefly affinity for conifer forest habitat limits their availability to Sierra meadows where conifer forest is found close by. Orthoptera are rarely encountered in non-meadow habitat (Beal 1912, Drost et al. 2003, Durst et al. 2007) but were found in Utah mountain meadow diets (Unpublished data) where grass/forbs vegetation is abundant. Coleoptera food items are a large part of non-meadow diets (Beal 1912, Drost et al. 2003) but were only occasionally found in Sierra meadow diets.

Food/Habitat Relationships

Although willow shrubs and water are the source for the majority of food production within meadows, Willow Flycatcher also took advantage of food items from other habitats when the opportunity presented itself. Some territories such as STAMPEDE-1 and PERR-6 offered a high abundance of terrestrial food items from grass/forbs and conifer forest habitat. Although grass/forbs vegetation is not thought to produce a high abundance of food in Sierra meadows, it likely plays a supplementary role in many meadows. The expansion of the foraging boundary into conifer forest habitat surrounding meadows may be unique to Sierra meadows and may be a response to declining food production within many meadows.

How important is aquatic habitat for food production in Sierra Nevada meadows?

The importance of aquatic habitat in Sierra Nevada meadows is indicated by the diversity of aquatic food items found within the diet. The assortment of aquatic insects from mayfly to deerfly are representative of the aquatic habitat environments found in Sierra meadows. Streams (medium and fast moving) are important for producing prolific aquatic insect hatches that Willow Flycatcher took advantage of in Milton Meadow. I have observed flycatcher targeting mayfly hatches in Utah mountain meadows (unpublished data) in a manner similar to that observed in Milton Meadow, providing further evidence of the importance of aquatic insect hatches to Willow Flycatcher in meadow environments. Standing water habitat, such as found in abandoned channels (oxbows) and near beaver dams were also important in producing food items such as deerfly, damselfly, and dragonfly. Similar habitat in Arizona was identified as producing

Odonata and Diptera food items, providing an important supplementary food resource (Wiesenborn and Heydon 2007).

Foraging Behavior

Overall, hawking and gleaning foraging methods were used equally in meadows although foraging method did vary across territories and meadows. Hawking was much more common in meadows were aquatic food was abundant and less common in meadows were terrestrial food was abundant. This pattern was also observed by Frakes and Johnson (1982) who found that gleaning was much more common in dry shrub habitat compared to wetter riparian habitat. Previous observations of Willow Flycatcher foraging in Sierra meadows (Sanders and Flett 1989) and in Washington (Frakes and Johnson 1982) indicate that hawking is the preferred foraging method. Although hawking is generally thought to be more common in meadows, gleaning can dominate in meadows where terrestrial food items such as grasshopper are more frequently foraged.

Willow Flycatcher were often observed foraging outside of territory boundaries in this study, especially at Milton and Perazzo meadows, suggesting that foraging outside of territory boundaries may be common in Sierra meadows. Sanders and Flett (1989) also found that Willow Flycatcher often foraged outside of territory boundaries, especially during the nestling stage, and occasionally foraged as far as 300 meters outside of territories in the Little Truckee River meadows. Observations of Willow Flycatcher foraging outside of territory boundaries in Utah mountain meadows also suggest that foraging outside of territories may be common within meadows (Dietrich per obs.). Although foraging outside of territories but still within meadow boundaries appears to be common, foraging outside of meadows may be uncommon and only occur when foraging

within the meadow is not possible (Dietrich per obs.). Willow Flycatcher consistently foraged in conifer forest outside of the Perazzo and Milton meadows and it appears that this behavior may be more common than previously thought within Sierra meadows. It is not clear why flycatcher are choosing to forage outside of the meadow but it could be the result of decreased foraging opportunities within the meadow caused by meadow degradation. Many meadows in the Sierra Nevada are drier than they were in the past (Green et al. 2003) and may limit aquatic food production within the meadow necessitating foraging outside of the meadow.

Diurnal Diet and Foraging Behavior

Diurnal variation in foraging location and targets may be related to food item availability. Mayfly and snakefly were targeted in the morning and evening, whereas leaf hopper and moth caterpillar were foraged more often in the middle of the day. Some food items such as wasp, damselfly, dragonfly, and deerfly were foraged equally throughout the day and thus may fill a more consistent role in the Willow Flycatcher diet in the Sierra Nevada. Similar diurnal trends were also found in Utah meadow diets (unpublished data) with food items being unequally foraged throughout the day. The diurnal trends found in this study reinforce the importance of diverse habitat and food sources that might be accessed throughout the day by foraging Willow Flycatcher.

Do different foraging strategies exist during the day within Sierra Nevada meadows?

Four foraging strategies were identified based on foraging method, food items, foraging location, habitat, and time of foraging. The first foraging strategy involves targeting aquatic hatch insects (mayfly, caddisfly, and stonefly), typically found outside

of the territory. The hawking foraging method is preferred, and foraging occurs in the evening and morning near fast- and slow-moving streams. The second foraging strategy occurs throughout the day in locations dominated by standing water and shrubs. Commonly aquatic (dragonfly, damselfly, and deerfly) and terrestrial food items (moth caterpillar, wasp, and leafhopper) are targeted. A mix of gleaning and hawking from short distances is preferred and occurs most often within the territory near beaver and oxbow ponds. The third foraging strategy targets terrestrial food items (grasshopper and ladybug beetle) during the midday and involves gleaning food items from sedge and grass/forbs vegetation near the ground and occurs both within and outside of the territory. The fourth foraging strategy typically takes place outside of the meadow in the conifer forest and involves gleaning terrestrial food items from tree branches and pine needles. Foraging occurs in the morning and evening and takes place only in territories that are close to surrounding conifer forest.

Sierra Nevada Meadow Management and Restoration Implications

Understanding habitat-food production relations is a strong basis for defining and maintaining effective habitat for Willow Flycatcher. The principles outlined below provide guidance to managers and restoration practitioners who are tasked with creating more foraging opportunities and meeting the food requirements of Willow Flycatcher in Sierra meadows.

(I) Aquatic meadow habitat is instrumental in meeting the food needs of nesting Willow Flycatcher.

Aquatic food can be a substantial portion of the Willow Flycatcher diet, representing at least 20% and in some cases is more than half of the diet. Aquatic habitat

includes oxbow ponds, beaver ponds, and streams. Streams can produce large aquatic insect hatches that are targeted by Willow Flycatcher. Standing water habitat provides habitat for dragonfly, damselfly, and deerfly, which are a staple part of flycatcher diet. Proper management of meadow hydrology includes protection of key hydrologic processes such as floodplain inundation and groundwater recharge in order to maintain aquatic habitat within meadows. Protection and restoration of fluvial geomorphic processes (avulsion, etc.) and features (oxbows, etc.) helps create the diverse aquatic habitat needed for food production. Stream and meadow systems with active sediment transport and channel dynamics can be self-sustaining and capable of maintaining important natural stream processes that meet the present and future food needs of nesting Willow Flycatcher in Sierra Nevada meadows.

(II) Increased habitat complexity within meadows increases foraging opportunities for nesting Willow Flycatcher.

Willow Flycatcher are opportunistic foragers and will often take advantage of diverse habitat within and near territories. For instance, Willow Flycatcher are more likely to benefit from having both standing and moving water habitat within or near a territory where they can benefit from both aquatic hatch insects as well as aquatic insects such as dragonfly, damselfly, and deerfly. Nearby forest or grass/forbs habitat can supplement the diet with terrestrial food items such as snakefly or grasshopper. Management and restoration actions focused only on aquatic habitat in meadows may unintentionally decrease important and diverse foraging opportunities and food item diversity. If restoration transforms meadows from a mix of standing and moving water into a habitat dominated by just standing water, the range of foraging opportunities may

be reduced, limiting the ability of flycatcher to supplement their diet with food items such as mayfly, snakefly, and grasshopper. Meadows that offer a mix of foraging opportunities and a diverse assortment food items are more likely to meet the overall and diurnal food needs of Willow Flycatcher in Sierra Nevada meadows.

(III) Foraging habitat outside of territories can be important for meeting the food needs of nesting Willow Flycatcher.

Observations of Willow Flycatcher foraging indicate that foraging can often take place outside of territory boundaries. This is consistent with previous observations of Willow Flycatcher foraging outside of territory boundaries, especially during the nestling stage (Sanders and Flett 1989). Managers should consider habitat within and adjacent to meadows as potential foraging habitat, even if outside of habitat requirements specific to Willow Flycatcher territories. Willow Flycatcher can and will forage outside of their territory and may even forage outside of the meadow. Management and restoration plans that prioritize the protection and enhancement of diverse habitat within and surrounding meadows, even if it does not meet territory habitat requirements, is important in providing foraging opportunities for nesting Willow Flycatcher. This principle stresses the importance of identifying and protecting important habitat and habitat features not only within territories but also outside of territories and surrounding meadows.

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CHAPTER IV

CONCLUSION

Requirements for willow shrub density and coverage have been established for Willow Flycatcher nesting habitat. Although water and saturated soil are common elements of Willow Flycatcher habitat in Sierra Nevada meadows, specific requirements for nesting habitat have not been defined. As the Willow Flycatcher population in the Sierra Nevada continues to decline, the need for well-defined habitat requirements has never been more urgent. Restoration practitioners and managers need a clear picture of suitable Willow Flycatcher habitat. Further, an understanding of how hydrologic conditions support suitable nesting habitat increases our ability to create and maintain Willow Flycatcher habitat.

In this study, hydrologic condition, along with vegetation and invertebrates were measured in 17 sites occupied by nesting Willow Flycatcher, as well as in 17 sites that had been occupied in annual surveys between 1997 and 2010 but are no longer used, and in 17 sites that had never been observed to be used by nesting birds. Occupied territories have 88% to 100% areal coverage of standing water and saturated soil, including roughly a quarter of the territory in deep standing water. Herbaceous vegetation within occupied sites was dominated by sedge vegetation and food that is desired by Willow Flycatcher was highest within occupied sites. An important question in our research was why abandoned sites are no longer occupied given that at one time they were. Seven of the abandoned sites did not fall within the saturation and sedge vegetation ranges observed for occupied sites. Of the remaining ten abandoned sites, the quality of willow shrubs was found to fall below the range required for flycatcher occupation. Recent restoration

within these meadows increased water levels and caused willow shrubs to be water stressed and die, making once-suitable habitat no longer adequate for nesting. These sites may recover, but growth of suitable willow shrub density and coverage will take years, perhaps decades.

From direct video of adult birds feeding their nestlings, as well as field observations of foraging behavior, the diet of meadow Willow Flycatcher differs from the diet observed in non-meadow habitats outside of the Sierra Nevada. Meadow diets have a larger abundance of aquatic food items (mayfly, damselfly, and dragonfly) and moth larvae. Snakefly appear to be unique to Sierra Nevada meadow diets. At sites with conifer forest adjacent to the meadow, snakefly was observed to be a large portion of the overall diet. Diet preference changed through the day with snakefly and mayfly being foraged on more often in the morning and evening and moth caterpillar and leaf hopper being foraged on during the middle part of the day. The presence of snakefly in the diet shows that Willow Flycatcher were willing to forage long distances and outside of territory boundaries. Willow Flycatcher also foraged outside of territory boundaries to reach fast flowing streams with mayfly hatches. Foraging behavior varied within meadows and territories throughout the day with some meadows being dominated by hawking and foraging outside of territory boundaries whereas others were dominated by gleaning and foraging within territory boundaries. Water and willow shrubs supported most of the food production within the meadows and appear to be particularly important elements in Willow Flycatcher habitat in the Sierra Nevada. Aquatic habitat features such as streams with fast flowing water and ponded features (oxbows, beaver ponds) appear to be

important in producing aquatic food insects and attracting terrestrial insects to territories and meadows.

The main goal of this research was to better understand Willow Flycatcher habitat in Sierra Nevada meadows and determine the optimal conditions needed for nesting Willow Flycatcher. Through this study of habitat requirements, diet, and foraging behavior four main insights were developed. 1) Willow Flycatcher in the Sierra Nevada favor territories that are almost entirely covered by standing water or saturated soil, including some deeper standing water. 2) Aquatic food items are an important part of Willow Flycatcher diet and their abundance is tied to wet conditions within meadows. 3) Aquatic habitat features such as fast moving water and standing water are needed to provide a diverse selection of aquatic food items. 4) Occasionally foraging occurs outside of the territory, most often in the morning and evening.

Willow Flycatcher habitat in the Sierra Nevada is a necessary mix of wet meadow and shrub habitat. This combination can be sensitive to changes in meadow hydrology and may be difficult to reproduce through restoration. Efforts to restore Willow Flycatcher habitat have not reduced the decline in bird population. A particular challenge in restoring meadows from a dry, incised condition is the need to maintain willow shrub habitat while rewetting the meadow. Restoration projects may accomplish rewetting at the expense of the quality of shrub vegetation. The coverage and density of robust willow shrubs must be maintained during rewetting or a strategy is needed to regrow appropriate willow shrub habitat after the hydrology is changed. The future of the Willow Flycatcher population in meadows of the Sierra Nevada depends on successful restoration projects in degraded meadows of the Sierra Nevada. The hydrologic conditions identified for Willow

Flycatcher nesting habitat, along with willow shrub requirements, provide guidelines for management and restoration of Willow Flycatcher habitat in Sierra Nevada meadows.