Relationships between Willow Flycatcher and Beaver-Modified Stream Reaches in Sierra Nevada Montane Meadows

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Point Blue

The INSTITUTE for BIRD POPULATIONS

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Cover photo

Blown-out beaver dam in the Walker River watershed. Jason Gregg / Point Blue.

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INTRODUCTION

The Willow Flycatcher is a highly imperiled breeding bird species in California. The Sierra Nevada Willow Flycatcher is one of two distinct breeding populations in the state. The Sierra population presently occurs in small numbers and within a limited number of meadows (<100) in the Sierra Nevada and Southern Cascades (Loffland et al. 2014). Recent estimates suggest there are fewer than 200 remaining breeding territories in the region, with the population nearly extirpated south of Lake Tahoe (Mathewson et al. 2011, Loffland et al. 2014). Though the population is dependent on montane meadows for breeding, meadow restoration has not reversed this alarming decline (Loffland et al. 2014). At this point we cannot assume that if we restore meadows the way we have been we will recover the Sierra population. One possibility is that factors outside of the breeding season may be limiting the species. Another, and not mutually exclusive, possibility is that we may need to better account for specific habitat needs of Willow Flycatcher when designing restoration projects.

Sierra Willow Flycatchers primarily breed in large wet meadows between 1000–2500 m in elevation. Sierra Willow Flycatchers typically select habitats with a complex mosaic of dense shrubs, primarily willow (*Salix sp.*) and alder (*Alnus sp.*), interspersed with open areas (Mathewson et al. 2013). The density of shrub cover is positively correlated with Willow Flycatcher presence at the nest site, territory, and meadow scales (Bombay 1999). Surface water or highly saturated soil that persists through much or all of the growing season are among the most important characteristics associated with breeding success and the birds tend to establish territories within the wettest microhabitats within a habitat patch (Mathewson et al. 2013).

Beavers modify meadows in ways that seem to increase habitat suitability for Willow Flycatcher. Beaver activities maintain surface water and wetter soils (Puttock et al. 2017), trap sediment and nutrients (Puttock et al. 2018), and encourage wetland-associated plant communities and mosaics while preventing tree encroachment (Cooke and Zack 2008, Wright et al. 2002) and discouraging nest predators (Cocimano et al. 2011). Our field-based observations and a survey of more than 100 meadows by Bombay (1999) suggest that meadows occupied by Willow Flycatcher are significantly more likely to have beaver present than meadows unoccupied by Willow Flycatcher. However, this observation has not been formally evaluated and there remains uncertainty about if and how the presence of beaver actually influences Willow Flycatcher occupancy and use of meadows.

We developed a study to address the question: Is the presence of Sierra Willow Flycatchers correlated with beavers and the intensity of their activity? We quantified and contrasted habitat attributes created and influenced by beavers in meadow stream reaches occupied and unoccupied by Willow Flycatcher and built a resource selection function to test Sierra Willow Flycatcher selection for beaver activities. Our findings have significant implications for the prioritization and design of meadow restoration projects for Sierra Willow Flycatcher.

METHODS

Willow Flycatcher Data

In 2014 we conducted an exhaustive review of Willow Flycatcher survey and occupancy data to determine current status and range of Willow Flycatchers in the Sierra Nevada and southern Cascade region (see Loffland et al. 2014 for detailed description of methods). We integrated data from multiple data sources to create a GIS layer and database of all Willow Flycatcher detections by date. For the current study, we started with the occupied meadows from the Desert Terminal Lakes (DTL) geography that were identified in Loffland et al. (2014). We then added detailed nest and territory location data collected during the Willow Flycatcher demography study that ran from 1997–2010 (Mathewson et al. 2011), and from more recent surveys of occupied, historically occupied, and information gap areas by The Institute for Bird Populations in the DTL in 2013–2018 (Strohm and Loffland 2015, Loffland and Siegel 2017, Schofield et al 2018). Surveys, territory mapping and nest searching followed standard protocols (Bombay et al. 2003, Mathewson et al. 2013). We then created a polygon layer in ArcMap that consolidated all known territory boundaries (n = 589) and nest locations (n = 403) from 2005–2017 in the DTL geography, as measured in the field using GPS or digitized in ArcMap from hand-drawn field notes (data from Mathewson et al. 2013, or subsequent H. Loffland unpublished data). Nest locations were buffered by a 40 m radius to estimate area utilized by flycatchers. The resulting occupied habitat polygon layer included only those portions of meadows that were known to be utilized by Willow Flycatchers from 2005–2017.

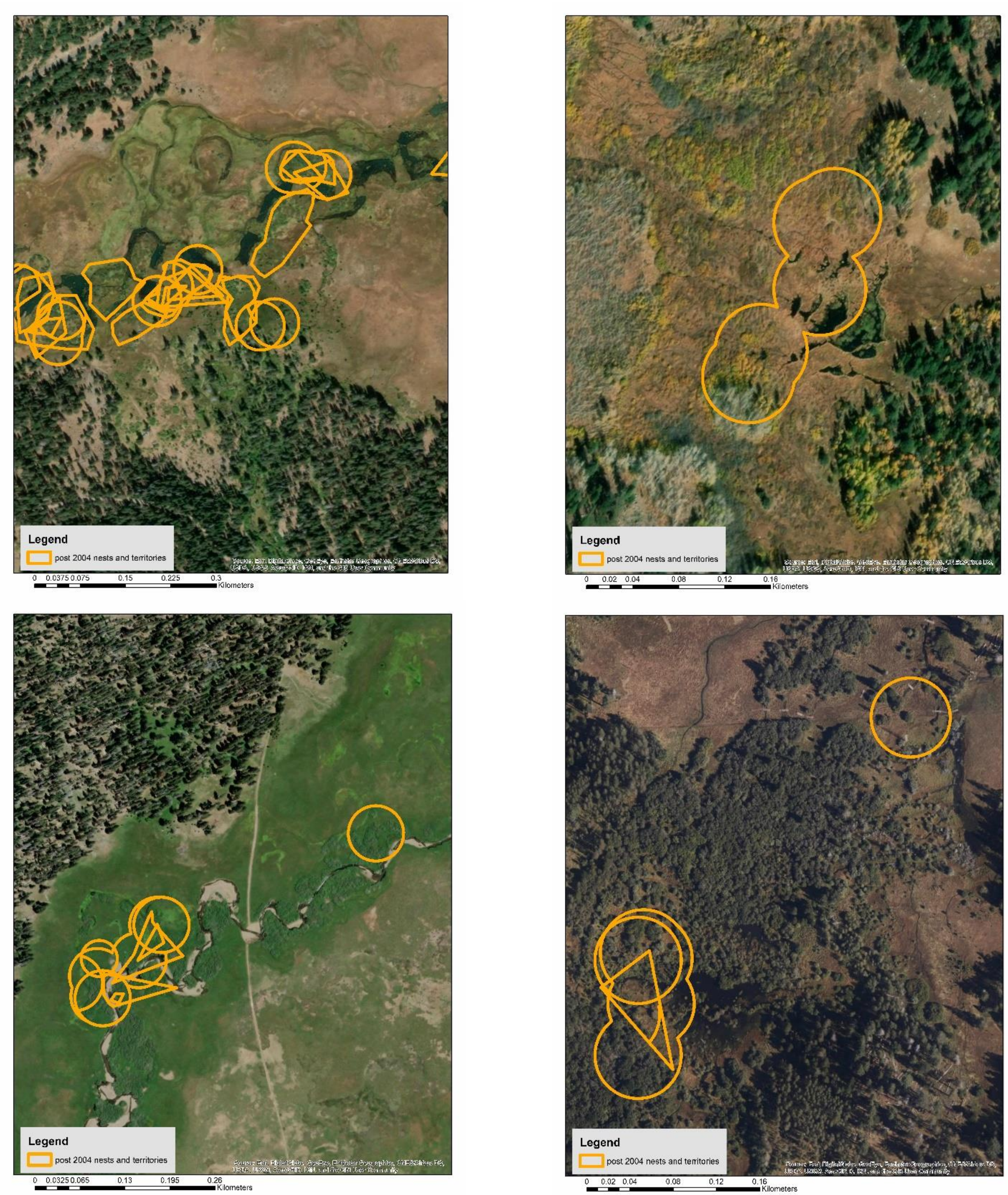

Figure 1. Examples of portions of meadows occupied by Willow Flycatchers (orange polygons) used in sample selection.

Site Selection

Given that Willow Flycatcher occupancy was rare across the study area, to maximize our sample in Willow Flycatcher occupied sites, we used a case-control sample design in which we drew a random sample of locations occupied by Willow Flycatchers and a second random sample of unoccupied locations. We identified a stream reach of approximately 300 m as the sample unit. This sample unit coincides with the model output of the Beaver Restoration Assessment Tool (Macfarlane et al. 2017), the primary basis of our sampling universe. The reach scale is also better matched to a Willow Flycatcher territory or territory cluster than is an entire meadow.

First we identified Willow Flycatcher-occupied meadows. Willow Flycatcher-occupied meadows were defined as those with a history of >1 territory and remained occupied past 2004. We partly used 2004 as the cutoff year because NAIP imagery was first available for CA in 2005, so we could investigate changes in habitat through time if we needed to for future analysis.

At Willow Flycatcher-occupied meadows we used BRAT model output, delivered to us in June 2018 by our collaborators at Utah State University, to further refine occupancy at the reach scale. We selected all reaches within 100 m of Willow Flycatcher territories and nests documented since 2005, or the nearest reach to the territory or nest when all reaches were >100 m away. When multiple reaches were within 100m, the reach with the larger peak flow recurring at a 2-year interval (Q2) was chosen. The reach with the smaller Q2 was identified as an adjacent reach, and removed from the pool of unoccupied reaches (see below). All Willow Flycatcher-occupied meadows and reaches occurred in the Truckee, Tahoe Basin, and Upper Carson watersheds; none were in the Walker River watersheds, despite recent detections. For occupied reaches in two meadows, Independence Lake meadow and Red Lake Peak meadow, the location of the stream reaches in the BRAT model (derived from the National Hydrology Dataset [NHD]) did not reflect on-the-ground knowledge of where the stream reaches occur, so we edited the reach placement by hand digitizing in ArcGIS (v10.5; ESRI 2017) to reflect on-the-ground realities. We then summarized the range of Q2 flow, reach slope, average baseflow (Qlow), stream power at average baseflow, and stream power during Q2 flows from the BRAT model output for Willow Flycatcher-occupied reaches. We also summarized the range of elevations and meadow sizes for Willow Flycatcher-occupied meadows from the Sierra Nevada Multi-Source Meadow Polygons Compilation (SNMMPC v2.0; UCD & USFS 2017).

To create the pool of unoccupied reaches, we selected all reaches throughout the DTL that met the following criteria based on Willow Flycatcher-occupied reaches and meadows:

a. ≤ to the maximum reach slope
b. ≥ to the minimum Q2 flow
c. ≤ to the second-highest Q2 stream power (the highest Q2 stream power of 4610 in the occupied reaches appeared to be a miscalculation due to NHD line placement error, hence use of the with second highest)
d. ≤ 50 m of a meadow in SNMPPC v2.0 (50 m buffer dealt with mismatches of stream and meadow digitization)
e. ≥ the minimum meadow size (as digitized in SNMPPC v2.0)
f. within the range of meadow elevations

We originally planned to further filter the unoccupied pool of reaches based on modeled beaver dam capacity. We planned to set a threshold of existing capacity score of ≥4 dams per km, but after noticing that a few of our Willow Flycatcher locations were in reaches with lower predicted beaver dam capacity, we reconsidered. Based on consultation with the BRAT team, we decided to use stream power instead of existing beaver dam capacity to inform selection of unoccupied sites.

We further limited the unoccupied pool of reaches to those on publicly accessible lands and within 1 km of a road. We identified all reaches in the unoccupied pool that intersected the holdings layer in the CA Protected Areas Database (CPAD). Most reaches with mixed public-private ownership were dropped. Additional reaches on city-owned lands not identified in the CPAD in the Tahoe Basin were hand-attributed by H. Loffland and B. Campos as publicly-accessible. We then filtered out all reaches > 1km of a road using the roads layer from the BRAT model output, which was derived from the TIGER roads layer. Lastly, we then attributed all unoccupied reaches adjacent to Willow Flycatcher-occupied reaches as "occupied-adjacent" reaches that were effectively removed from the available sample, to help meet the assumption that all reaches in the unoccupied pool were known to be unoccupied.

We selected sample locations in the unoccupied and occupied reach pools using the grts.line function in the package SDraw in the program R (v3.5.1; R Core Team 2018).

For the unoccupied pool, GRTS-selected reaches that were less than 200 m in length were "adjoined" (adjacent reach also selected) to a directly adjacent reach of less than 200 m in length if available, or we moved the selection to a directly adjacent reach >200m in length if unavailable (in this latter case, if two reaches <200m in length were available, one was randomly selected with a coin flip). If a GRTS-selected unoccupied reach obviously did not have willow (riparian deciduous shrubs) within 100m based on aerial imagery, but a directly adjacent reach in the same meadow did, we moved the selection to the adjacent reach instead of dropping the selection; if it was unclear whether willow was present within a 100m based on aerial imagery, the reach was retained. If a reach was determined to not have willow present when visited in the field, the reach was dropped.

For the occupied pool, GRTS-selected reaches that were less than 200 m in length were "adjoined" (an adjacent reach also selected) to a directly adjacent reach of less than 200m in length if available, or moved the selection to a directly adjacent reach >200m in length if unavailable (in this latter case, if two reaches <200m in length were available, one was randomly selected with a coin flip). GRTS-selected reaches were also dropped in GRTS-priority order if: (1) the resultant sample polygon (see below) did not intersect an after-2004 nest polygon or territory, or (2) if the resultant sample polygons for two adjacent reaches greatly overlapped (>50%), or (3) when the resultant sample polygons for two adjacent reaches overlapped and if by dividing the overlapping area among the polygons one polygon no longer intersected a territory or polygon.

For all selected stream reaches, we used the add geometry tool in ArcMap (v10.5; ESRI 2017) to add a start, mid, and endpoint to each reach, then drew two line segments among the three point, and dissolved the line segments into one line for each selected reach. We then buffered the line by 100 m (planar, flat end). The resultant polygon was clipped by the SNMPPC v2.0 layer, then hand-corrected to match the edge of the meadow or the 100-m buffer distance, whichever was smaller.

We randomly distributed habitat survey points within each sample polygon. Survey points were distributed at a density of 1/ha of the polygon. For the largest polygons (6.5–7.3 ha), we capped the number of points to 6 and for the smallest (1.2–2.5 ha) we had a minimum of 3 points. Points were distributed to within 20 m of the edge of the polygon (negative 20 m buffer on the sample polygon) at least 20 m apart using the Create Random Points tool in ArcMap.

Data Collection

We trained four observers on the identification of beaver sign, beaver dams, and lodges, as well as data collection protocols, over the course of two days in the field in July, 2018. Observers were supplied with waders and rubber boots, GPS unit with reach polygon boundaries and releve points, rangefinder, digital camera, vegetation measurement stick (48″ long, ¾″ dia. wooden dowel ringed with black marker at 10 cm intervals, with a thick ring at 1 m), maps of reaches, and data forms. At each polygon, data collection was separated into two phases.

First, observers performed a complete area search of each reach polygon looking for dams, lodges, and other beaver sign, always starting the area search at the downstream end of the reach. They recorded several attributes for each beaver dam. Upon discovery of a dam they recorded the location using GPS, and assigned each dam a unique ID. Observers recorded the status of each dam as: intact, breached, or blown-out. Breached dams were defined as those with a large notch in them, but the breach was not the full height of the dam. Blown-out dams were breached through the full height of the dam. Observers recorded the location of each dam relative to the main channel. Dams that were not on the main channel were designated as being on secondary channels or on the floodplain. They measured the maximum height of the dam from the lowest point in the channel just downstream of the dam to the top of the dam. If the downstream channel was not well defined, they walked the length of the dam to find the tallest point relative to the downstream side. They used a laser rangefinder to measure the length of the dam (perpendicular to flow) in meters. Observers recorded whether the dam was actively being maintained or inactive based on the presence or absence of fresh cuttings and pool water close to the full height of the dam. Observers also recorded the location of each lodge. They assigned a unique ID to each lodge and recorded whether the lodge was actively being maintained or inactive based on the presence or absence of fresh cuttings on the lodge. Finally, observers recorded several other signs of beaver activity within the reach polygon, including cut stems, tracks, skid trails, felled trees, or "corn cobs" (stems with all bark chewed off). They noted age of the activity as fresh (that spring or summer) or old (anything older than that). Observers also took a photo of each dam and lodge.

After the area search was completed, observers navigated to all the random habitat survey points in the plot. We measured the vegetation and other habitat conditions within a 20-m radius of the point location. In the rare occasion that access to the exact point centerwas not possible because it was located in a deep pond, observers got as close as they could to the point and used the sampling radius plotted on a paper map and the GPS unit to assess the original sampling area from an accessible location. We used a relevé method to assess habitat conditions. We made visual estimates of vegetation cover and height in the three vegetation layers: herbaceous, shrub, and tree. We estimated relative cover of each species for the tree and shrub layers and the relative cover of forb, grass, and sedge/rush species in the herbaceous layer. We also estimated the percent of the plot surface in each of the first three soil water condition categories, below. We did not record the percent of meadow surface that was moist or dry, but we provide their definitions for context.

Moving –surface completely covered in water and water has detectable flow

Standing – surface completely covered in water and water has no detectable flow

Saturated – no standing water at surface, but soil has a visible sheen, is easily penetrable, and water pools around your foot when you step on it

Moist – moisture visible and felt in the soil, but it is not easily penetrable

Dry – no moisture content visible or felt in the top 2" of soil; if you were to shovel it, it would be dusty

Analysis

We contrasted attributes of beaver dams at Willow Flycatcher occupied versus unoccupied sites in multiple ways. First, we calculated beaver dam density as the number of intact, breached, and blown-out dams, both active and inactive, divided by the plot area searched surrounding each reach. Beaver dam density was used as an index of beaver activity and beaver-caused modification of the stream reach. We compared the dam heights and lengths in occupied versus unoccupied sites using a two-sample t-test. Lastly, we used weighted logistic regression contrasting beaver dam densities at Willow Flycatcher-occupied versus unoccupied sites to generate a resource selection function (Manly et al. 2002). We opted to not include any other habitat variables in this model because, despite their known importance for Willow Flycatcher habitat quality, because all of them were influenced by beavers (e.g. willow cover, conifer cover, soil saturation). We weighted observations of zeros (unoccupied) and ones (occupied) according to their relative sample sizes ($w_1 = 1$; $w_0 = n_1/n_0$; Russel et al.

2007). This weighting scheme treats the ratio of zeros to ones as an artifact of sampling with no biological significance, thus, weighting ensured that observations of 0s and 1s informed model parameter estimates equally, reflecting our case-control sampling design (Keating and Cherry 2004). Ideally, zeros in the data should represent unused sites not contaminated with misclassified flycatcher occupied sites (Keating and Cherry 2004). Because of intensive focus on Willow Flycatcher occupancy by resource managers in the Truckee and Carson River watersheds along with repetitive surveys by IBP, we are reasonably confident that unoccupied sites did not meet our criteria for occupancy. Additionally, as mentioned previously, we excluded reaches adjacent to known occupied reaches from the unoccupied pool, further reducing the potential for contamination of the occupied pool. We also dropped one unoccupied site in the Carson River watershed from analysis, given a Willow Flycatcher detection in 2016 and lack of prior monitoring at this site. We fitted weighted logistic regression models using the *glm* function in R (v. 3.5.1; R Core Team 2018). Given the rarity of Willow Flycatcher in the region and restrictive nature of our definition of occupancy, we assumed the probability of reach occupancy was less than 0.1 across our sampling universe, even at the highest recorded values of beaver dam densities (Zhang and Yu 1998). We then contrasted the probability of use given increasing beaver dam density to the probability of use given no beaver dams to yield the relative odds of Willow Flycatcher occupancy (aka. relative risk; Keating and Cherry 2004).

We derived plot-scale values of habitat variables measured at habitat survey points by taking the averages across sampling locations within each plot. We then compared willow cover, conifer cover, average shrub height, and soil saturation using a non-parametric Kruskal-Wallis test by ranks. Soil saturation was calculated as the sum of the moving water, standing water, and saturated soil categories.

RESULTS

We searched 35 Willow Flycatcher-occupied and 32 Willow Flycatcher-unoccupied reaches for beaver dams in July and August of 2018 (Figure 1). Most of the survey reaches were in the Truckee River and Lake Tahoe Basins, with fewer in the Carson River watershed, and only two in the Walker River watershed. The distribution of sample locations reflects the availability of montane meadow habitat on publicly accessible lands that met the criteria of our site selection filters, with more meadows farther north. Though we visited the southernmost sampling location, in Green Creek

State Wildlife Area, we had to drop in from the analysis given uncertainties in its historic occupancy status, leaving 31 unoccupied reaches.

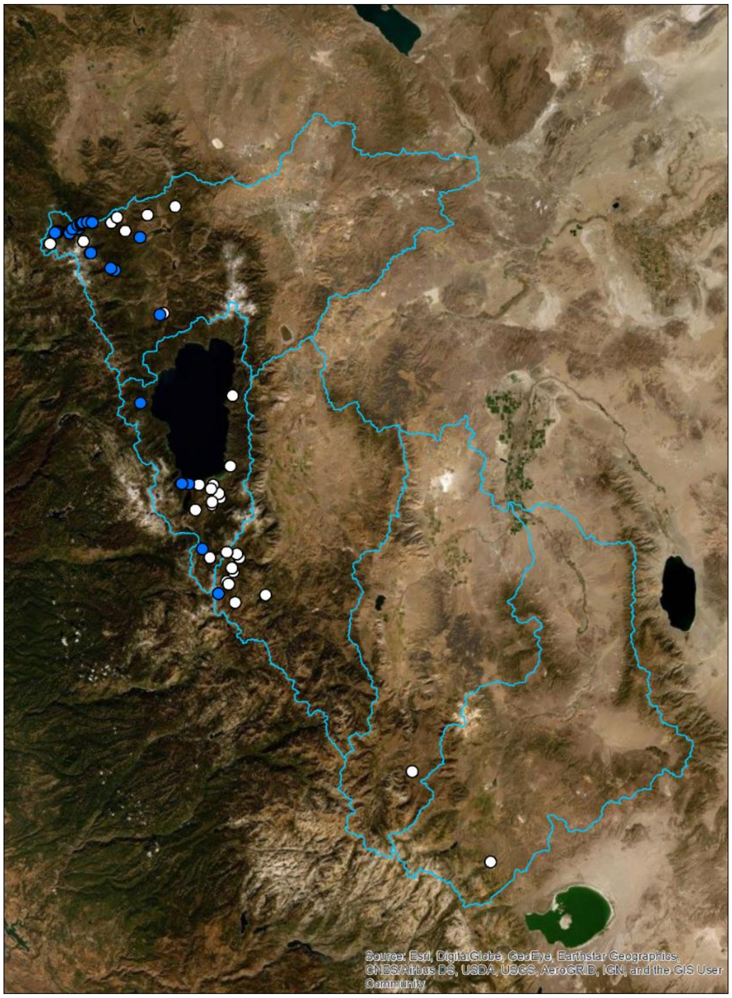

Figure 2. Study area map. Dots indicate visited sample reaches occupied (blue) and unoccupied (white) by Willow Flycatcher. Light blue outlines are the Truckee, Lake Tahoe, Upper Carson, West Walker and East Walker HUC 8 watersheds, from northwest to southeast, respectively.

We found and measured 114 beaver dams. Dam density appeared higher in occupied reaches (Table 1), but the median dam density in our occupied and unoccupied samples was zero, meaning over half the reaches in each sample had no beaver dams. Beaver dams ranged short to rather tall and narrow to very long (Table 1). There was some evidence dams were taller in occupied reaches (t = -1.729, P = 0.087) and little evidence dams were longer in occupied reaches (t = -1.538, P = 0.128).

Table 1. Attributes of beaver dams in stream reaches occupied and unoccupied by Willow Flycatcher.

Metric	Occupied	Unoccupied
N dams	78	36
mean dams density (min,max) [per hectare]	0.6 (0,3.4)	0.2 (0,1.6)
mean maximum height (min,max) [m]	0.6 (0.2,2.3)	0.5 (0.1,1.2)
mean total length (min,max) [m]	10 (1,61)	6 (1,55)
intact	54%	50%
breached	33%	31%
blown out	12%	19%

When we modeled the likelihood of Willow Flycatcher occupancy as a function of beaver dam density using a resource selection function, there was good evidence that Willow Flycatcher occupancy was positively correlated with beaver dam density (Figure 2, $z = 2.023$, $P = 0.043$). Willow Flycatchers were more than twice as likely to occupy a reach with 3 dams per hectare as a reach without beaver dams.

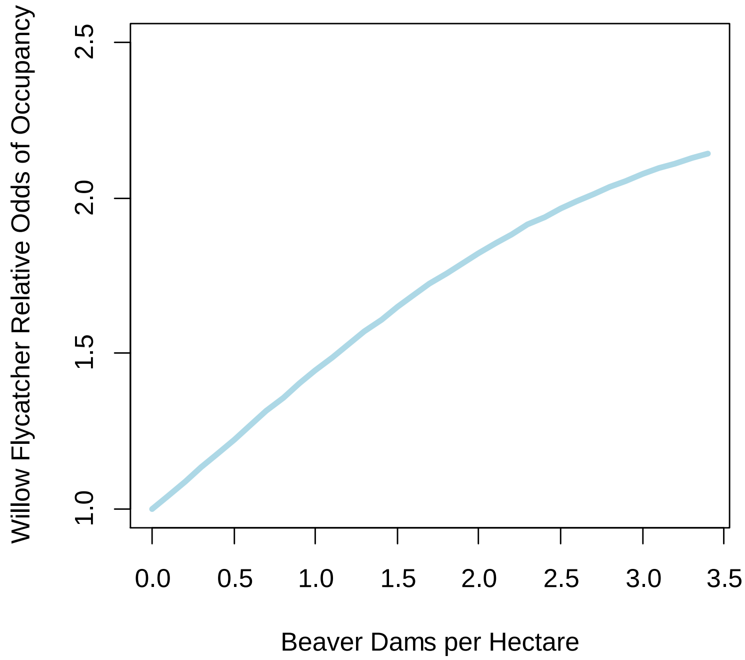

Figure 3. The likelihood of Willow Flycatcher occupancy increased with beaver dam density.

We found some differences in meadow habitat characteristics between reaches occupied and unoccupied by Willow Flycatchers. Occupied reaches had 129% higher median willow cover (W = 354, P = 0.010) and 143% higher median water cover (W = 317, P = 0.002) than unoccupied reaches (Table 2, Figure 4). There was no difference in shrub height (W = 513, P = 0.571; Table 2) between reach types and the minor apparent difference in conifer cover was biologically small with little statistical support (W = 651, P = 0.131).

Table 2. Characteristics of meadow habitat at stream reaches occupied and unoccupied by Willow Flycatcher.

Metric	Occupied	Unoccupied
N sites	35	31
median willow cover (Q1,Q3)	16 (12,25)	7 (3,15)
median conifer cover (Q1,Q3)	0 (0,0.7)	0.6 (0,3.6)
median water cover (Q1,Q3)	17 (8,31)	7 (2,20)
median shrub height (Q1,Q3)	1.8 (1.2,2.2)	1.7 (0.9,2.1)

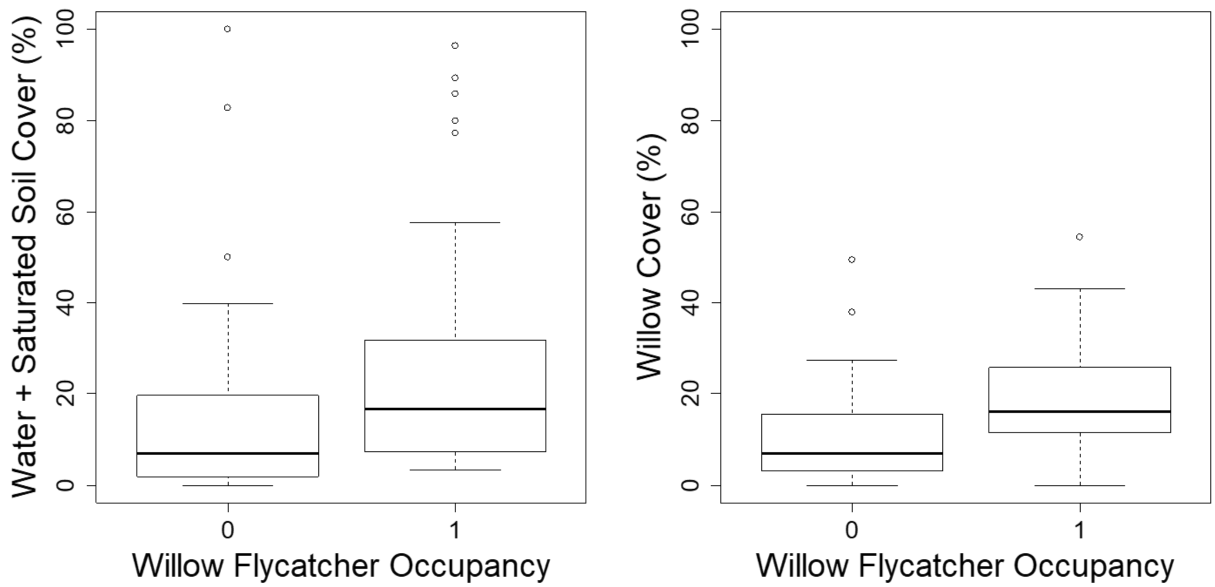

Figure 4. Box and whisker plots showing the distribution of water cover and saturated soil conditions (left panel) and willow cover (right panel) at stream reaches unoccupied (0) and occupied (1) by Willow Flycatcher. Each box represents the lower and upper quartiles, with median as horizontal dark line. Whiskers extend from the box no more than 1.5 times the inner-quartile range; values beyond are plotted as dots.

DISCUSSION

Our results support the conclusion that beavers and their activities are important for Sierra Willow Flycatcher. Our findings complement others' that suggest beavers promote the restoration of (Southwestern) Willow Flycatcher and increased densities of other riparian birds (Albert and Trimble 2000, Cooke and Zack 2008). Our results also suggest that restoration practitioners, public land managers, and private land owners can improve Willow Flycatcher habitat by encouraging beavers and their activities, and potentially mimicking them, in montane meadows.

Our metric of dam density in the resource selection function was an index of beaver activity. That is to say, it represents how much beavers have modified a given reach in ways Willow Flycatchers find attractive. This includes modifications to wetted area, willow and other riparian shrub cover, conifer encroachment, tree cover, primary productivity, insect abundance, and likely others we do not yet understand.

Beaver dam analogs (BDAs) are a tool used by restoration practitioners that mimic a subset of beaver activities (Pollock et al. 2007). We do not know how well BDAs substitute for beavers from the perspective of Willow Flycatchers, but we do know that installing BDAs results in wetter conditions with more ponded water that in turn promotes higher primary productivity (Pollock et al. 2014, Silverman et al. 2019), attributes selected by Willow Flycatchers (Hatten et al. 2010, Mathewson et al 2013). Our results suggest that BDAs installed at a density of 2–3 per hectare would best mimic the dam densities that maximize occupancy by Willow Flycatcher. To provide context to this dam density recommendation, the density of dams installed in the BDA treatment reach at Childs Meadow was approximately 1.1 per meadow hectare within 100 m of Gurnsey Creek. When installing BDAs, our results also indicate that increasing the dam height and length may be better for Willow Flycatcher, as there was some evidence that beaver dams were taller and longer in Willow Flycatcher occupied reaches. Even if these relationships with larger dams are not real, it would be prudent to install BDAs with lengths and heights representing the distribution of beaver dams we measured to best mimic beaver activities. We recommend that the ultimate goal for BDA-based restoration projects should be to encourage and retain occupancy by beavers, as BDAs are not a complete substitute for beaver activities. Beavers are present on-site at all times to actively maintain water levels. Beavers create canal networks to safely extend their access to forage. Beavers heavily prune willows and other riparian shrubs, creating a mosaic of shrub heights, age classes and extent. Beavers slowly raise heights of dams. And when their dams blow-out, they may or may not rebuild them.

Focusing beaver-based restoration efforts on meadows and areas that are highly suitable for both Willow Flycatcher and beavers will maximize the likelihood of Willow Flycatcher occupancy. Our experience with the BRAT model in this study area suggests most montane meadows in the range of Willow Flycatcher had stream reaches classified as highly suitable for beavers (≥5 dams/km; the frequent and pervasive categories in BRAT). Beaver habitat suitability in these meadows seemed limited primarily by high stream power and insufficient riparian habitat (woody riparian vegetation) for forage and dam building materials. Successful meadow restoration should increase the quality and extent of riparian habitat (see recommendations on willow planting below), so stream power then becomes the primary limiting factor in most montane meadows in the range of Willow Flycatcher. The meadow characteristics that restrict high suitability Willow Flycatcher habitat, on the other hand, are far more numerous (Loffland et al.

2014). Because of this, when targeting restoration for Willow Flycatcher, we recommend first prioritizing restoration at the meadow scale based on previously developed guidelines (Loffland et al. 2014). Stream power can then inform which main-channel or tributary reaches within the meadow would be best for beaver-based restoration techniques and riparian shrub planting. Even on reaches with prohibitively high stream power, unmapped (in the BRAT model output) secondary/high-flow channels on the floodplain may provide good opportunities for beaver-based restoration methods after the primary channel is restored. Tributaries to the main channels within meadows should not be overlooked. Many sites currently occupied by Willow Flycatcher and beaver are smaller tributaries because the larger, high-flow primary channels in the meadow is incised and undammable by beaver and therefore lacking in habitat components required by Willow Flycatcher. All restoration projects should also include planting willows in high densities and protecting willows from grazing pressure to ensure sufficient forage and dam-building materials for beavers and habitat for Willow Flycatchers. Large extents of high density plantings better enables beaver use of the willows while retaining willows of sufficient densities and height for Willow Flycatcher nesting.

Our sample design has three notable implications for the interpretation and application of our results. Firstly, the results of our study are applicable to the range of conditions we sampled. Though we sampled only in the Truckee, Carson, and Walker river drainages, meadow conditions in these watersheds are representative of Willow Flycatcher habitat throughout the Sierra. For example, we have observed the majority of Willow Flycatcher occupied sites in the largest remaining population cluster for this species in the Sierra/Cascades region (Lassen cluster) to be in close association with beaver modified stream reaches (R. Burnett pers. obs.). And, though we had an upper elevation limit on our sampling frame representing the highest elevation meadow meeting our criteria for Willow Flycatcher occupancy, our results very likely apply to higher elevations, which become more important in context of climate change.

Secondly, our decision to filter the unoccupied pool of stream reaches by the presence of willow or alder cover means that the reported increases to the relative odds of Willow Flycatcher occupancy with increasing dam density are in reference only to stream reaches with at least one willow or alder present. The many meadow stream reaches in the Sierra that are devoid of willows or alders have no chance of Willow

Flycatcher occupancy and are not the reference condition for the results of our resource selection function. We do not know what the probability of occupancy is for a reach in our sample with at least one willow or alder present and no beaver dams, but we are confident it is less than 10% and suspect it is less than 5%. We undoubtedly would have found a stronger effect of beaver dam activity on Willow Flycatcher occupancy if we had not filtered by willow presence. However, by excluding those reaches without willow or alder, the presence of which is the most basic prerequisite for Willow Flycatcher occupancy, we could further emphasize and isolate the importance of beaver activity with a limited sample size.

Lastly, we chose to count and include in our analysis not only intact and breached beaver dams, but blown-out dams as well. Incorporating blown-out dams into our tally allowed us to buffer against uncertainty in changes of occupancy by beavers since reaches in our Willow Flycatcher occupancy pool last had flycatchers present. Nonetheless, because of the time lapse between data collection (2018) and our threshold year of occupancy (2005 or later) it is still possible that we recorded no beaver dams at reaches in our Willow Flycatcher occupancy pool that were actually occupied by beavers and their dams when Willow Flycatchers were present, but since then also lost the beavers. In other words, in order to have a sufficiently large and diverse pool of Willow Flycatcher occupied reaches, we set the threshold year to 2005, but did so at the expense of potentially diluting the effect of beaver dam density on flycatcher occupancy because of the temporal disconnect between flycatcher occupancy and field data collection. Recording blown-out beaver dams also allowed us to capture the dynamic nature of dams at Willow Flycatcher occupied reaches that should be taken into consideration when designing restoration projects. Dewatered former beaver ponds are known to promote bird and floristic diversity in Quebec (Aznar and Desrochers 2008).

While we suggest the use of this information to inform Willow Flycatcher conservation throughout the Sierra Nevada and southern Cascades, replicating this study in the two largest remaining population clusters for this species in the region would be valuable. Of the 200 estimated remaining Willow Flycatcher territories in the region, two-thirds occur within the Lassen and McCloud clusters. Current occupancy is well understood at least within the Lassen cluster, where productivity is highest in the region (Matthewson 2013), and thus meadow restoration is a high priority.

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