RESEARCH ARTICLE

Bird response to hydrologic restoration of montane riparian meadows

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Montane riparian meadows foster biodiversity and support critical ecosystem services. A history of exploitation has left most riparian meadows throughout the Mountain West of the United States with incised channels, severely compromising their functionality. Hydrologic restoration of riparian meadows aims to increase overbank flow during spring run-off and elevate groundwater levels in the dry season. Outcome-based evaluations of the dominant meadow restoration methods are lacking and needed to ensure objectives are being met and to guide modifications where needed. We completed 1,282 point count surveys from 2009 to 2017 at 173 sampling locations across 31 montane riparian meadows in California restored using partial channel fill techniques (e.g. pond-and-plug) to evaluate the expected outcome of increased abundance of meadow birds. We analyzed trends in abundance for 12 focal bird species from 1 to 18 years after hydrologic restoration, substituting space for time in our mixed effects Poisson regression models that included covariates for the amount of riparian deciduous vegetation (RDV) before restoration, stream flow, precipitation, and temperature. We found evidence for a positive effect of time since restoration on abundance for 6 of the 12 species. Although pre-restoration RDV cover was the most frequently supported predictor of abundance, high pre-restoration cover of RDV slowed response rates for only two species, suggesting other elements of hydrologic function are also important for meadow birds. Drawing on our results, we provide suggestions for enhancing hydrologic restoration efforts in riparian meadows so that benefits may accrue more quickly to more bird species.

Key words: birds, hydrologic restoration, montane meadows, partial channel fill, pond-and-plug, riparian restoration, Sierra Nevada

Implications for Practice

- Restoring elements of hydrologic function unrelated to riparian deciduous vegetation (RDV) for nesting and foraging appears to improve habitat quality for riparian meadow birds.
- Revegetation and management that accelerate the creation of large, high-density patches of RDV that maximized bird abundance in our study may accelerate bird response to hydrologic riparian meadow restoration projects.
- Species' relationships with climatic gradients and stream flow can inform where restoration has the greatest potential to benefit montane riparian wildlife species by identifying geographies and localities where they may reach high abundance.

Introduction

Riparian meadows of the Sierra Nevada, Southern Cascades, and Warner mountain ranges (hereafter, collectively referred to as the Sierra Nevada) in California are small floodplains that, if hydrologically functional, retain water from high-flow events and slowly release it in summer months, maintaining stream

flow and groundwater levels at or near the land surface in an otherwise seasonally dry landscape (Loheide et al. 2009; Hunsaker et al. 2015). The interacting hydrological, geomorphological, and ecological processes of functional riparian montane meadows support biodiversity and provide critical ecosystem services including flood attenuation, water storage, water quality improvement, and carbon sequestration (Hammersmark et al. 2008; Norton et al. 2011; Purdy et al. 2011; Viers et al. 2013). Like the montane floodplains of larger, glaciated gravel-bed river systems of the United States and Canada (Hauer et al. 2016), the meadows and riparian areas of the Sierra Nevada are hotspots of biodiversity, with disproportionate use compared to their land area (Kattelmann & Embury 1996). Riparian corridors, including riparian meadows, comprise less than 2% of the Sierra Nevada (Kattelmann & Embury 1996;

Viers et al. 2013), yet 20% of the Sierra Nevada's terrestrial vertebrate species depend on them (Graber 1996). Many of the vertebrate species most closely associated with Sierra Nevada meadows are endangered, threatened, or declining due in part to a history of meadow alterations and exploitation, such as deliberate channel modifications and long-term over-grazing by livestock (Kattelmann & Embury 1996; Menke et al. 1996).

Across the broader Mountain West of the United States, 61% of streams have medium to high human disturbance and 41% have streamside vegetation communities in fair or poor health (U.S. EPA 2006). In the Sierra Nevada, the hydrological and ecological integrity of most montane meadow streams have been compromised (Kattelmann & Embury 1996; Menke et al. 1996), with many exhibiting severe channel incision (Hunsaker et al. 2015). Channel incision reduces the hydrological connection between streams and their floodplains and dewaters the meadow (Hunsaker et al. 2015). Because a larger volume of water is needed to initiate flow over the meadow surface, incised channels limit the processes of scour and deposition crucial to the succession of riparian plant communities (Ward et al. 2002). Incised channels also increase groundwater discharge from meadow aquifers to streams, resulting in lower water table elevations, decreased groundwater retention, and conversion of meadows from wetland to upland habitat types (Loheide & Gorelick 2007; Hunsaker et al. 2015). Without active intervention to re-elevate the water table and restore hydrologic connectivity between meadow surface and stream channel, heavily impacted meadows remain altered, resulting in a drastic loss of ecosystem services (Loheide et al. 2009). In growing recognition of the value of the ecosystem services provided by functional montane meadows, the state of California and large regional partnerships established ambitious meadow restoration goals (CNRA et al. 2016; Drew et al. 2016).

Hydrologic restoration of riparian meadows with incised channels aims to increase overbank flows during spring run-off and elevate groundwater levels in the dry season, with expected enhancement of the many ecosystem services provided by functional meadows (Hunsaker et al. 2015; Drew et al. 2016). However, resources are often lacking to evaluate whether restoration objectives for ecosystem services have been met at project sites. Because of the lack of rigorous and long-term evaluation (Ramstead et al. 2012) and sensitivity to variation in ecosystem context and methodology (reviewed by Hunsaker et al. 2015), the effectiveness of meadow restoration in achieving intended objectives is not well understood (cf. Hammersmark et al. 2008; Pope et al. 2015). Yet understanding the efficacy of meadow restoration in general, and specific restoration techniques in particular, in achieving desired outcomes is critical to maximizing the multiple benefits of restoration (e.g. Dybala et al. 2019b). Partial channel fill methods, including the pond-and-plug technique first used in California in 1995, have been the most frequently used for restoring the hydrology of riparian meadows of the Sierra Nevada and Southern Cascades since the mid-1990s (Wilcox et al. 2001; Hammersmark et al. 2008). Outcome-based evaluations of the dominant meadow restoration methods are needed to ensure objectives are being met and to guide modifications where needed.

A frequent objective of riparian meadow restoration is to increase the abundance of target bird species following expected increases in riparian habitat quantity and quality (Drew et al. 2016). Meadows have been called the single most important habitat for birds in the Sierra Nevada (Siegel & DeSante 1999), and three bird species listed as Endangered or Threatened by the state of California—Willow Flycatcher (*Empidonax traillii*), Great Gray Owl (*Strix nebulosa*), Greater Sandhill Crane (*Grus canadensis tabida*)—rely on montane meadows (CDFG 1994; Mathewson et al. 2013; Kalinowski et al. 2014). However, published evaluations of the long-term response of birds to riparian meadow restoration are lacking. Riparian restoration elsewhere in the western United States has resulted in clear benefits to bird abundance and diversity, primarily through increased structural complexity and abundance of vegetation, indicators of riparian habitat quality for birds (Kus 1998; Gardali et al. 2006; Golet et al. 2008; Rockwell & Stephens 2018). Yet these studies have largely focused on revegetation projects that did not restore or modify hydrologic connectivity (but see Dybala et al. 2018), the latter of which is the primary focus of most riparian meadow restoration projects.

We evaluated the expected outcome of increased abundances of birds following the restoration of hydrologic connectivity and revegetation in riparian meadows by assessing the rate of change in abundance of focal bird species at sites restored using partial channel fill techniques (e.g. pond-and-plug). We substituted space for time in our analysis to create a longitudinal history of 1–18 years after restoration. We assumed changes in bird abundance were in part attributable to vegetation structure created by the restoration project, and patterns and rates of change depended upon species-specific habitat requirements fulfilled as vegetation succession occurred over time. Specifically, we investigated: (1) which meadow-associated bird species responded to meadow restoration and at what rate and (2) how the cover of riparian deciduous vegetation (RDV) before restoration affected the rate of response. We expected bird abundance would increase with time since restoration and pre-restoration RDV cover. We also thought the rate of bird response following restoration may be slower in sites with higher pre-restoration RDV cover because of reduced potential to increase habitat quality through restoration.

Methods

Study Locations

We studied breeding birds at 31 montane riparian meadow restoration sites over 25 meadow complexes in the Sierra Nevada, Southern Cascades, and Warner mountain ranges of California (Table S1; Figs. 1 & 2). We selected these sites from known hydrologic restoration sites in riparian montane meadows implemented across this region between 1999 and 2015. No comprehensive list of meadow restoration sites existed, so we contacted restoration practitioners and land managers in our study region to compile a list of sites with already completed restoration projects. We identified 54 restoration sites using a similar pond-and-plug restoration method (Hammersmark et al. 2008). The
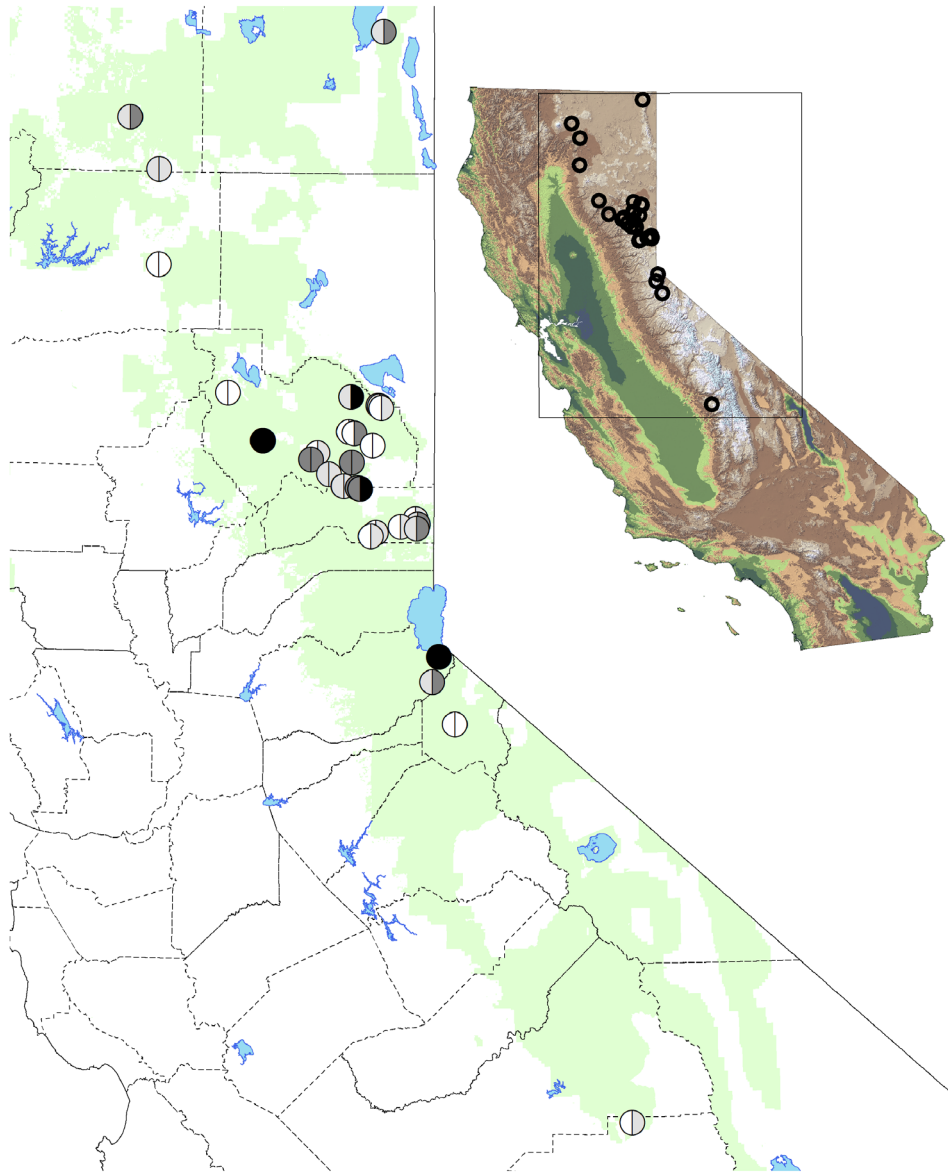
Figure 1 Location of 31 riparian meadow study sites with hydrologic restoration projects (circles) surveyed for birds in the Sierra Nevada, Southern Cascades, and Warner mountain ranges of California relative to National Forest boundaries (light green), counties (dashed lines), and large waterbodies (blue). Colors in the split circles represent the time since restoration (white, 1–5 years; light gray, 6–10 years; dark gray, 11–15 years; black, 16–18 years) monitoring started (left half) and ended (right half) at each study site.

sites on the list shared the common feature of partial channel fill of a previously incised channel, such that deep ponds, either a result of mechanical excavation or completely unfilled sections of incised channels, were present after restoration during spring run-off. Mechanically excavated borrow pits, present at 52 sites, were located on-channel, off-channel, or both. The form of the stream channel after restoration varied from a newly engineered channel to a remnant channel reactivated by the hydrologic restoration.

From this pool of 54 restoration sites we sampled birds at 31 sites (Table S1). These included 14 restoration sites at which we had already established post-restoration monitoring prior to

the conception of this synthesis, and an additional 17 sites restored between 1999 and 2009. We selected these 17 sites to maximize the spatial and temporal extent of our sample (Table S1). We were unable to access one additional selected site on private land. We had no previous knowledge of the ecological condition of the 17 additional sites during the selection process. We considered the boundaries of a restoration site to be the area in which the groundwater table was expected to be raised as described on project documentation, or, where this documentation was lacking, the upstream and downstream extent of channel fill and ponding within the riparian meadow. Riparian meadow was the dominant hydrogeomorphic type at
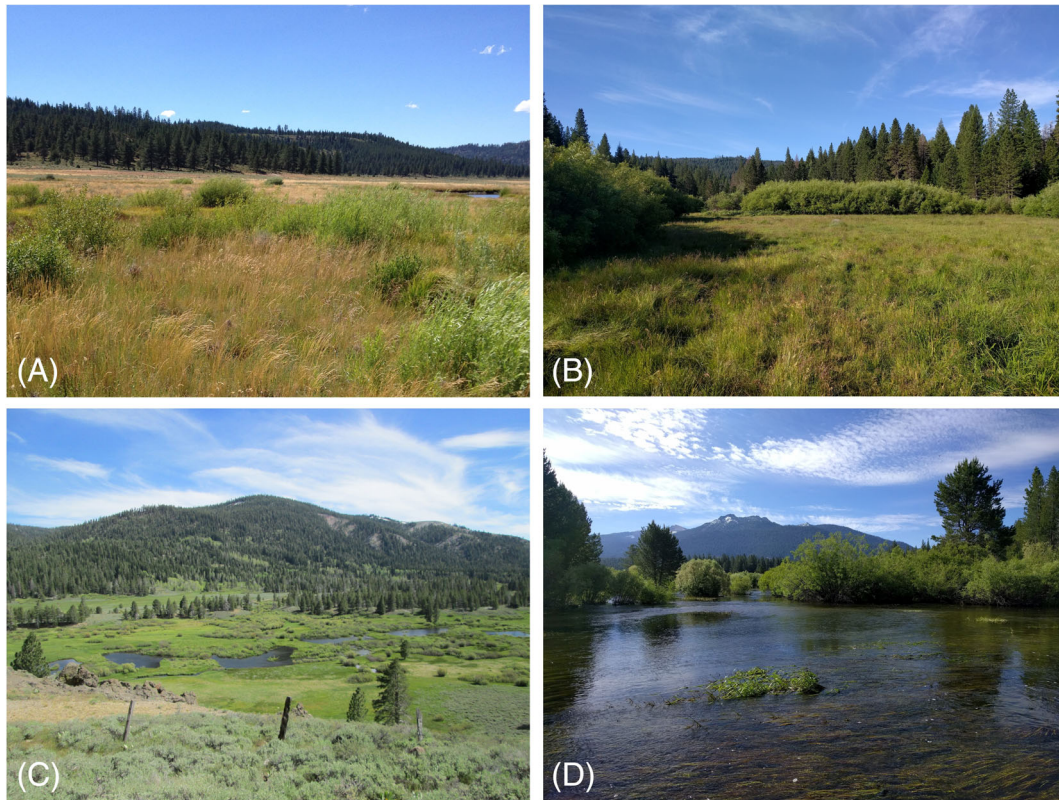
Figure 2 Examples of restored montane riparian meadow sites in the Sierra Nevada, California. (A) Growing willows at Ferris Fields restoration site, restored 2007, photo 22 July 2016 by BC. (B) Mature willows at Little Schneider Creek restoration site, restored 1999, photo 15 June 2017 by BC. (C) Flooded borrow pits at Perazzo Phase I restoration site, restored 2009, photo 30 May 2015 by HL. (D) Floodplain inundation at Trout Creek restoration site, restored 2001, photo 01 July 2017 by BC.

Table 1 Meadow focal bird species ordered by total number of detections within 100 m of observers.

Common name	Species name	Detections
Song Sparrow	*Melospiza melodia*	1,818
Yellow Warbler	*Setophaga petechia*	957
Warbling Vireo	*Vireo gilvus*	95
Wilson's Snipe	*Gallinago delicata*	74
Red-breasted Sapsucker	*Sphyrapicus ruber*	63
Black-headed Grosbeak	*Pheucticus melanocephalus*	52
White-crowned Sparrow	*Zonotrichia leucophrys*	49
Calliope Hummingbird	*Selasphorus calliope*	43
Willow Flycatcher	*Empidonax traillii*	41
Wilson's Warbler	*Cardellina pusilla*	36
MacGillivray's Warbler	*Geothlypis tolmiei*	31
Lincoln's Sparrow	*Melospiza lincolnii*	30
Swainson's Thrush	*Catharus ustulatus*	1

all sites (Weixelman et al. 2011). At each site we distributed sample locations ≥230 m apart while maximizing the number of locations in the restored area, resulting in 2–13 sample locations per site.

Bird Data

Surveyors conducted standardized 5-minute point counts at sample locations (Ralph et al. 1995). With the aid of rangefinders, surveyors estimated the distance to all individual birds at the time of initial detection. Protocols for recording distance to individual birds varied throughout the course of data collection. For 6% of visits, surveyors recorded whether individuals were within 50 m of the observers; for 40% of visits, surveyors categorized detections into distance bins of 0–10, 11–20, 21–30, 31–50, 51–100 m, and greater than 100 m; for 54% of visits, surveyors estimated an exact distance for detections within 300 m. We counted from sunrise up to 5 hours after sunrise, without counting in inclement weather (i.e. precipitation, fog, or high wind). All surveyors passed identification field tests with supervisors after at least 2 weeks of training to identify birds and estimate distances. Sample locations were visited up to twice in a given year from 26 May to 7 July, the period of peak songbird breeding activity in the study region.

We selected for analysis an a priori subset of 13 bird species (hereafter, focal species; Table 1; Campos et al. 2014). These species reach their greatest breeding abundance in montane meadow and riparian habitat in the study area, are appropriately sampled by passive point count methods, and were expected to respond positively to habitat conditions created or enhanced

by the restoration of meadow form and function, specifically: (1) floodplain inundation at a less than 2 year interval; (2) water table within the rooting zone of meadow plants for growing season, including some flooded or perennially saturated areas in secondary channels or other depressional areas; (3) vigorous herbaceous layer dominated by native obligate or facultative wetland graminoid species; (4) riparian deciduous shrubs with active recruitment; and (5) riparian deciduous trees. We detected one focal species, Swainson's Thrush, only once, so we dropped it from further consideration.

Environmental Data

We compiled data to describe the hydrology, climate, and habitat structure at restoration sites and at each of their individual sample locations for use in models of bird abundance (Tables 2 & S2). As an index for pre-restoration habitat quality, we estimated the pre-restoration cover of RDV (shrubs and trees) within a 50-m radius of each sample location using National Agricultural Imagery Program imagery from 2004 to 2014 viewed in ArcGIS (ESRI 2017), and imagery from 2000 to 2015 available in Google Earth (v 7.3.2). As an index of the amount of water flowing through the meadow at sample locations, we used StreamStats Batch Processor version 4.5 to estimate the peak flow at a 2-year recurrence interval at the nearest primary flow channel to each sample location (Ries et al. 2017). We used the 2014 California Basin Characterization Model for the 1981–2010 period (Flint et al. 2013) to describe climatic variation across the elevational and latitudinal gradients of sampled meadows over which our focal species' abundance and occurrence are known to vary (Siegel et al. 2011). These climatic variables included the June–August average daily maximum temperature at the restoration site, and the average annual precipitation in the watershed area upstream of each restoration site, as an index of watershed wetness.

We also sampled vegetation characteristics in the field for use as detection covariates in bird abundance modeling. Restoration sites sampled for birds over a span of six or more years were sampled twice for vegetation, whereas others were sampled once. Vegetation sampling occurred July–August and utilized a relevé protocol to visually estimate the percent cover of shrubs within 50 m of each sample location.

Analysis

Shrub cover varied among sites and within sites (Table S2). Comparisons of point count data collected from samples with different vegetation structure can be confounded by differences in bird detectability (Buckland et al. 2001). We used the *Distance* package in R to estimate detection probability for each focal species as a function of shrub cover, the primary potential source of obstruction for visual and auditory cues. We corrected for the effect of shrub cover on detection to decrease the likelihood of type II error. Shrub cover was expected to increase over time, leading to decreased detection probability. Uncorrected abundance estimates in our regression model could therefore be biased low at increasing time since restoration, potentially leading us to incorrectly conclude no effect of time since restoration. We detected little to no change in shrub cover at those sites we surveyed twice for vegetation, so we averaged the shrub cover estimates from both vegetation surveys. For the 94% of our point count data where we recorded exact or binned distances to birds within 100 m, we fit detection curves for each bird species using five distance bins—0–10, 11–20, 21–30, 31–50, 51–100 m—with a uniform key function, a half-normal key function, and a hazard-rate key function. We selected the best detection model for each species using AIC and the *Distance* package's model diagnostic plots (Buckland et al. 2001). We then integrated the selected detection model over 0–50 m to estimate the average detection probability within 50 m for each of the sample locations in the dataset for each species, based on the shrub cover measured at each location. The predicted detection probability for each species at each sampling location was used as an offset in the next modeling step

Table 2 Variables included in abundance models for meadow birds after meadow restoration. See text for detailed information on data sources. * indicates variable used to model detection probability, included as an offset term in the abundance models.

Variable (code)	Scale	Description	Data Source
Time since restoration (tsr)	annual	Number of years since restoration was completed	Restoration project documentation and restoration practitioners
Pre-restoration /initial riparian deciduous vegetation (irdv)	sample location	Percent cover of riparian deciduous shrubs and trees prior to or at the time of restoration within 50 m of point count sample location	Aerial imagery
Stream flow (sflow)	sample location	Flow of a 2-year flood event at main stream channel nearest each point count sample location (cubic feet second^{-1}), log-transformed	USGS StreamStats Batch Processor version 4.5
Temperature (tmx)	restoration site	Average June through August maximum daily temperature at restoration site (°C)	California Basin Characterization Model
Precipitation (ppt)	restoration site	Average annual precipitation in watershed upstream of each restoration site (mm)	California Basin Characterization Model
Percent cover of shrubs (shrubcov)*	sample location	The percent cover of all shrubs within 50 m of each sample location	Field-collected

(Hedley et al. 2004), allowing us to include all of our point count surveys. We opted not to propagate the error around estimates of detection probability into the abundance models (e.g. Buckland et al. 2009) because doing so would not have influenced type II error. Because the uniform key function was selected as the top model for Wilson's Snipe (suggesting detection was unrelated to shrub cover) and because we were unable to fit a detection model for Lincoln's Sparrow, we excluded offset terms from the abundance models for these species.

We hypothesized focal species abundance would increase with pre-restoration RDV cover, and, if restoration enhances the quality and quantity of riparian habitat, time since restoration. We also anticipated a possible interaction between time since restoration and pre-restoration RDV cover because of reduced potential to increase habitat quality through restoration at sites with higher pre-restoration RDV cover. No effect of time since restoration would suggest a species was either little affected or not affected in a consistent way by restoration, data were insufficient to detect a response, or, a species' response was immediate following restoration and changed little with time thereafter. We hypothesized relationships to stream flow and climatic variables would be variable across focal species.

To estimate the effect of time since restoration and environmental variables on focal species abundance, we built generalized linear mixed models with Poisson error and logarithmic link function using the package *lme4* version 1.1-20 (Bates et al. 2015) in program R x64 version 3.5.1 (R Core Team 2018). Our sample unit was a single-point count survey visit and the dependent variable was the count of a focal species within 50 m. We also included a random intercept for each location nested within each restoration site and a random intercept for year of data collection. We implemented a three-step model selection process for each species. First, we selected between linear and quadratic forms of each fixed effect: time since restoration, pre-restoration RDV cover, stream flow, temperature, and precipitation. We compared a univariate model with a linear term to a model with both a linear and a quadratic term using a likelihood ratio test, repeating this for each fixed effect. Second, we ran a full model with each fixed effect and an interaction between time and pre-restoration habitat. The full model included the main effect of the interaction term and quadratic terms as applicable according to the results from step two. Variables in the full model were not highly correlated ($r < 0.25$). Lastly, we compared the full model with and without the interaction term, and, as applicable, quadratic terms, using a likelihood ratio test, comparing higher-order terms sequentially, starting with the interaction term. We retained higher-order terms when supported ($p < 0.1$). We used z scores of coefficients in the final models to assess the importance of variables in describing bird abundance. We standardized all continuous predictors with a mean of zero and standard deviation of one.

Results

We completed 1,282 point counts from 2009 to 2017 at 173 sampling locations across 31 restoration sites, with all 31 sites visited in both 2016 and 2017. We sampled birds at each restoration site 2–17 times over 1–9 years post-restoration. Detections of Song Sparrow and Yellow Warbler dominated our focal species detections, comprising 55 and 29% of all detections, respectively (Table 1). The relationship of detection probability with shrub cover was mostly negative and mixed in its strength among species (Table S3). Variation around the estimated effect of shrub cover was large for several species, but there appeared to be a clear negative effect of shrub cover on the detection of Song Sparrow, Yellow Warbler, Warbling Vireo, and Willow Flycatcher.

Measured environmental condition varied among restoration sites, and to a lesser extent, within restoration sites (Table S2). The pre-restoration percent cover of RDV ranged 0–65%, the 2-year peak stream flow ranged 44–686 cfs, average annual precipitation ranged 620–1,524 mm, average June–August maximum daily temperature ranged 20.3–29.7°C, and shrub cover during bird surveys ranged 0–65% (Table S2).

We found evidence for a positive effect of time since restoration on abundance of six species, though model certainty was low for two of them (Table 3). Abundance of Yellow Warbler, Warbling Vireo, Song Sparrow, Wilson's Warbler, Black-headed Grosbeak, and Red-breasted Sapsucker were predicted to increase annually by 10, 11, 25, 70, 93, and 103%, respectively (Table 3; Fig. 3). The high response rates for the three least prevalent species reflect extremely low abundance (i.e. near absence) at year 1 (Tables 1 & 3). For Yellow Warbler and Warbling Vireo, these response rates were calculated at mean values of pre-restoration RDV cover because both species' response rates decreased with increasing RDV prior to restoration, driven by a negative interaction between pre-restoration RDV cover and time since restoration (Table 3). Yellow Warbler response declined from 13 to 4% annually when the pre-restoration RDV cover was 1 vs. 40%, respectively. Warbling Vireo response declined from 16 to 1% annually when the mean pre-restoration RDV cover was 1 vs. 40%, respectively. For the 6 other species, evidence was insufficient or lacking to suggest a relationship between abundance and time since restoration (Table 3; Fig. 3). The coefficient for White-crowned Sparrow suggested a possible negative relationship with time since restoration ($p = 0.12$), but uncertainty around the estimate was high.

Pre-restoration cover of RDV was an important predictor of abundance for 10 species (Table 3; Fig. S1). These relationships were positive for nine species, though models for five species supported an additional negative quadratic term with abundance plateauing or declining at the highest values (>40% cover) of pre-restoration RDV cover, or in the case of MacGillivray's Warbler, a clear modal relationship with abundance peaking at 20–30% cover of pre-restoration RDV cover (Table 3; Fig. S1). Wilson's Snipe was negatively correlated with pre-restoration RDV cover (Table 3; Fig. S1).

Stream flow and climatic variables were important in describing abundance patterns across our study area for most species. Stream flow was an important predictor of abundance for seven species, with negative relationships for three species (Table 3; Fig. S2). Average annual precipitation was an important predictor of abundance for seven species; first-order linear

Table 3 Parameter estimates (and SEs) for selected weighted generalized linear mixed models of annual abundance of bird species, time since restoration (tsr), and various environmental variables at montane meadows in California. Variables are defined in Table 2. * indicates $p \leq 0.1$ based on z-test for difference from zero. ** indicates $p \leq 0.05$ based on z-test for difference from zero.

Parameter	Black-headed Grosbeak	Calliope Hummingbird	Lincoln's Sparrow	MacGillivray's Warbler	Red-breasted Sapsucker	Song Sparrow	Warbling Vireo	White-crowned Sparrow	Willow Flycatcher	Wilson's Snipe	Wilson's Warbler	Yellow Warbler
intercept	−4.9 (0.67)**	−2.61 (0.44)**	−4.64 (0.49)**	−2.87 (0.69)**	−2.48 (0.5)**	0.92 (0.13)**	−3.7 (0.46)**	−5.95 (0.96)**	−7.51 (1.37)**	−3.73 (0.37)**	−5.01 (0.69)**	−0.61 (0.24)**
tsr	0.66 (0.25)**	0.19 (0.26)	0.19 (0.34)	0.06 (0.41)	0.71 (0.25)**	0.23 (0.05)**	0.40 (0.24)*	−0.58 (0.37)	0.17 (0.34)	0.1 (0.24)	0.53 (0.32)*	0.37 (0.12)**
irdv	0.7 (0.22)**	0.14 (0.18)	0.58 (0.22)**	1.58 (0.45)**	1.21 (0.29)**	0.89 (0.12)**	1.56 (0.29)**	0.58 (0.24)**	0.58 (0.54)	−0.42 (0.21)**	0.86 (0.28)**	0.96 (0.16)**
irdv²	—	—	—	−1.21 (0.41)**	−0.25 (0.13)**	−0.24 (0.06)**	−0.38 (0.14)**	—	—	—	—	−0.24 (0.08)**
sflow	−0.02 (0.45)	−0.87 (0.25)**	−0.63 (0.26)**	−0.31 (0.42)	0.63 (0.31)**	0.3 (0.1)**	−0.56 (0.28)**	0.15 (0.48)	0.76 (0.66)	0.77 (0.31)**	−0.22 (0.39)	0.63 (0.18)**
tmx	0.69 (0.47)	0.02 (0.19)	−0.77 (0.24)**	0.26 (0.35)	0.13 (0.3)	0.17 (0.09)*	0.08 (0.24)	−1.42 (0.68)**	0.05 (0.47)	−0.11 (0.26)	−0.61 (0.33)*	0.2 (0.17)
ppt	0.18 (0.44)	1.49 (0.42)**	0.85 (0.31)**	1.26 (0.62)**	1.26 (0.61)**	−0.03 (0.1)	0.61 (0.29)**	0.14 (0.63)	1.23 (0.54)**	0.44 (0.26)*	0.6 (0.38)	0.02 (0.16)
ppt²	—	−0.79 (0.32)**	—	−1.34 (0.59)**	−1.12 (0.44)**	—	—	—	—	—	—	—
tsr:irdv	—	—	—	—	—	−0.23 (0.14)*	—	—	—	—	—	−0.13 (0.05)**

relationships were positive for all seven, and models supported an additional negative quadratic term for three of these species, with abundance peaking at 1,000–1,200 mm (Table 3; Fig. S3). Temperature was an important variable for four species, with negative relationships for three species (Table 3; Fig. S4).

Discussion

Riparian meadow restoration using partial channel fill techniques resulted in increasing abundances of half of the focal bird species over time. No species clearly responded negatively to restoration. Positive response rates were strongest for rarer species that were largely absent early in the post-restoration time period, and for Song Sparrow, the most abundant species in our dataset. Song Sparrow require dense herbaceous vegetation and minimal RDV development before habitat is suitable for near-ground nesting close to or over water (Arcese et al. 2002), conditions created soon after hydrologic restoration.

Warbling Vireo and Yellow Warbler were the only species exhibiting decreased response rates with increasing pre-restoration RDV cover, supporting the idea that there is reduced potential to increase habitat quality for these species through hydrologic restoration at sites with high RDV cover. The lack of evidence that other species' response rates were affected by pre-restoration RDV cover suggests their response to restoration was primarily or equally driven by something other than RDV cover, such as depth to water table or herbaceous vegetation density. In this case, restoration focused solely on revegetation of RDV would not achieve the full benefits of restoration to birds in our study.

The large and relatively consistent effect of the cover of RDV on species abundance at the time of restoration suggests vegetation growth following hydrologic restoration contributes to increased bird abundance over time. Cover of RDV prior to restoration was the most frequently supported predictor of focal species abundance. Our results support the conclusions of previous studies that positive outcomes for birds in riparian restoration projects are in part realized through increased structural complexity and abundance of vegetation (e.g. Krueper et al. 2003; Golet et al. 2008; Earnst et al. 2012). Structural vegetation complexity in meadow and other riparian systems enhances insect food resources (Ramey & Richardson 2017) and provides cover from direct and nest predation (Ammon & Stacey 1997). Tall willows in riparian areas are particularly attractive to many species we studied (Bombay et al. 2003; Rockwell & Stephens 2018). Though increasing RDV may come with an apparent tradeoff of reduced abundance of one focal species—Wilson's Snipe, with possibly similar ramifications for Sandhill Crane which select open, inundated areas of meadows for nesting (Littlefield 1995)—restoring the RDV component of riparian meadows is critical to ensure positive outcomes for all other focal species.

We suggest several ways land managers may increase meadow restoration outcomes for focal bird species. First, restoring meadows in geographies where focal species tend to occur in higher abundance will likely result in the largest gains in population size. Relationships with stream flow and
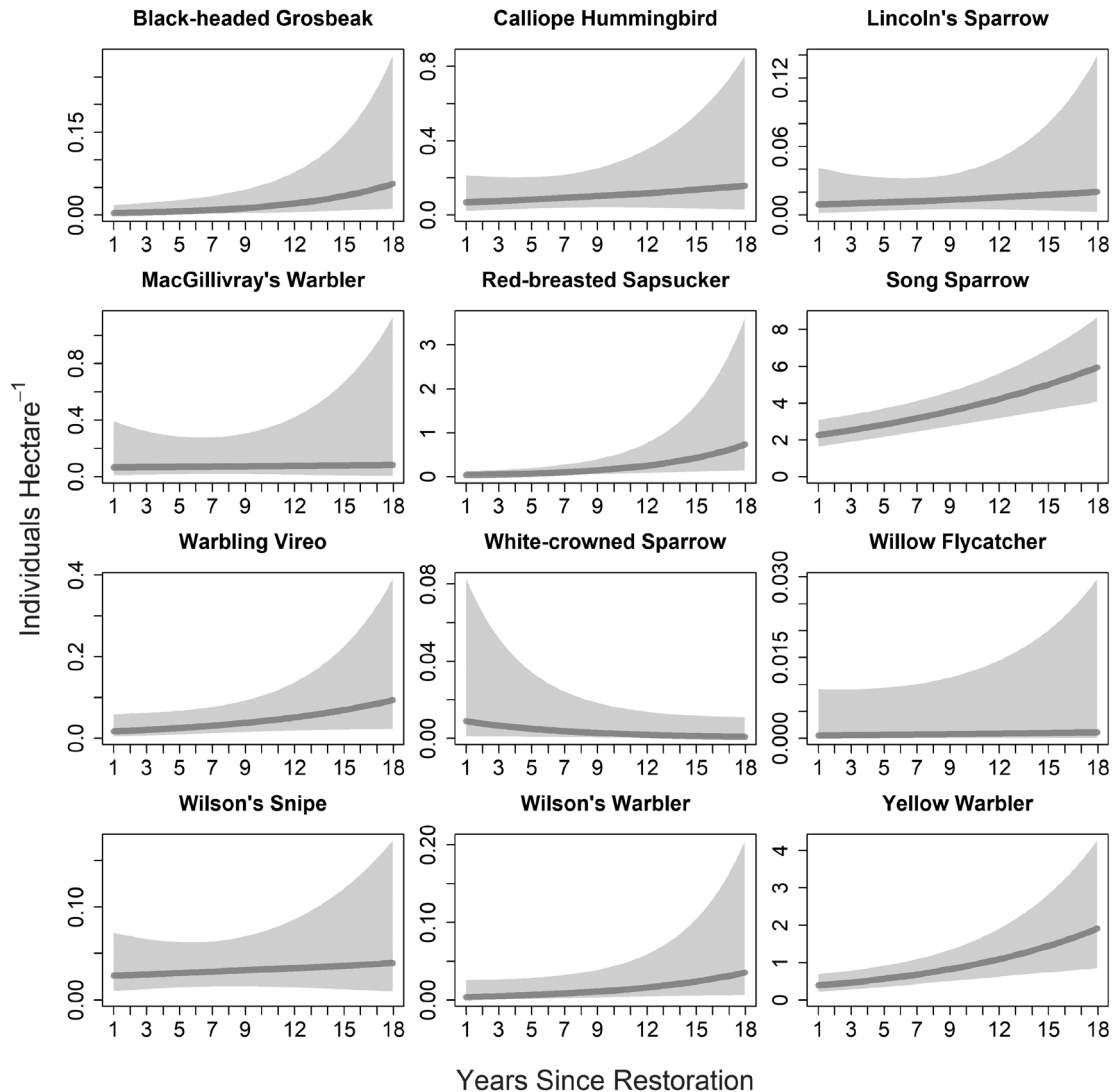
Figure 3 Mean predictions and ±95% CI for the marginal effect of time since restoration on abundance for 12 bird species across 31 restoration sites. All other parameters were held at mean values. Scientific names are in Table 1.

temperature were mixed among species, so prioritizing meadows for restoration based on those variables, while possible, would result in trade-offs among species. In contrast, relationships with precipitation were more consistent and suggest restoring meadows with moderate or higher average annual precipitation would provide greater benefits to the majority of focal species relative to more arid sites. The abundance of meadow focal species is maximized at meadows with 1,300–1,750 mm of precipitation in the upstream watershed (Campos et al. 2014), yet only 20% of the restored meadow sites in this study had precipitation in that range.

Second, if the rate of response to montane riparian meadow restoration by most focal bird species is partially driven by the rate of development of vegetation structural complexity, then restoration actions that accelerate that development should increase the rate of bird response. Most of the sites in our sample were not actively revegetated with RDV or, if they were,

planting occurred at low densities. Increased planting of RDV during restoration and, as necessary, subsequent protection from browse during seedling and sapling stages, would likely accelerate results for birds. A primary objective for many montane meadow restoration projects in the Sierra Nevada region is to improve or create Willow Flycatcher habitat, yet restoration plans and on-the-ground actions frequently address only the hydrologic component of Willow Flycatcher habitat. Given the continued decline of this species despite considerable restoration effort over the last two decades, land managers may need to place additional focus on planting, recruiting, and protecting RDV, in addition to resolving hydrologic problems at restoration sites. Other research indicates habitat creation in riparian restoration sites is jump-started by planting riparian shrubs and trees, with the initial growth of aboveground carbon stocks more than double those sites without a replanting component (Dybala et al. 2019a). *Salix* and *Populus* species are of primary

importance given their role as a component of bird habitat and as passive ecosystem engineers in riparian areas (Corenblit et al. 2007). However, revegetating with other RDV species representative of functioning reference sites is encouraged given dispersal limitations of some plant taxa and the potential ecological value of a broader plant community (Zobel et al. 2006; González et al. 2015), such as plants that support nectar resources for pollinators, including hummingbirds.

Lastly, restoring sites in close proximity to established populations of target bird species may also help to accelerate the reestablishment of populations at the restoration site (Gardali & Holmes 2011). For example, Kus (1998) found the occupation of restored riparian sites by the endangered Least Bell's Vireo was hastened by the presence of adjacent habitat with breeding populations of vireos. Prioritizing restoration based on proximity to established populations is likely important for the endangered Willow Flycatcher, which is now patchily distributed, thereby limiting dispersal potential (Loffland et al. 2014; Schofield et al. 2018).

Though our results provide evidence for positive trends toward recovery of bird populations at meadow restoration sites, they do not provide evidence for fully functional riparian meadow systems or full recovery of bird populations after hydrologic restoration. Though bird abundance usually reflects habitat quality (Bock & Jones 2004), this assumption is not always valid (Van Horne 1983). Information on reproductive success and survival would provide greater evidence that restoration sites are truly supporting viable populations. In the Sierra Nevada, Willow Flycatcher reproductive success increased with increasing willow cover at multiple spatial scales (Bombay et al. 2003), supporting the idea that increased shrub cover following restoration may increase reproductive output for this and other meadow bird species.

It is unclear how well populations of focal bird species indicate for other taxonomic groups or ecosystem processes in riparian meadow systems. Previous research, that did not include birds, suggests no single ecological attribute in meadow ecosystems indicates well for meadow condition (Purdy et al. 2011). We agree with Purdy et al. (2011) that evaluating multiple ecological attributes of management and restoration interest provides the best assessment of meadow condition, a sentiment echoed by others in the context of evaluating the success of ecosystem restoration in general (Ruiz-Jaen & Aide 2005; McDonald et al. 2016). Pond-and-plug restoration of riparian montane meadows appears to meet objectives for hydrological processes (Hammersmark et al. 2008; Hunsaker et al. 2015), however, this and other similar meadow re-watering techniques may be falling short of achieving objectives for channel condition and surface soil carbon stores (Pope et al. 2015).

Detecting an effect of time since restoration in our analysis and attributing that effect to the success of the restoration actions depends on several assumptions. We assumed changes in bird abundance were largely attributable to changes in resources and habitat characteristics affected by time since restoration, such as food (e.g. insects; Golet et al. 2008), the structural complexity of vegetation (Trowbridge 2007), and predation (Cocimano et al. 2011). However, management actions that alter meadow habitat after restoration could cause a deviation from an unaltered trajectory. For example, sites in our study were variably grazed by livestock (primarily cows but also sheep), ranging from none to intensive. Grazing removes plant biomass and can negatively impact riparian and meadow bird habitat (Taylor 1986), potentially inhibiting its establishment or delaying its maturation (Opperman & Merenlender 2000). In this context, grazing could reduce the rate of bird response to restoration or even negate it (e.g. Krueper et al. 2003). We also assumed no larger-scale population trends contributed to the time-since-restoration response and species had the capacity to increase their populations locally in response to improved habitat quality. This capacity may vary depending on the ecological traits of the species, such as its fecundity, dispersal, competitive ability, and conspecific attraction (Ward & Schlossberg 2004; Rodríguez et al. 2007; Mathewson et al. 2013) and the proximity of potential source populations; we acknowledge some of these assumptions may not have been met for Willow Flycatcher (Schofield et al. 2018) given its declining status throughout our study region and extirpation from much of its former range (Loffland et al. 2014). Lastly, it is important that the response curves we report are interpreted within the temporal scale of our study. While 18 years is a relatively long span for assessing response to restoration, the recovery of these meadows is likely to continue for decades, which will likely continue to influence the trends in bird abundance. Species that showed strong responses during our study interval are likely to plateau, whereas those showing little response may respond rapidly once a habitat suitability threshold for them is reached.

Our comparison of avian response among restoration sites was based on a space-for-time substitution, without assessing bird species abundance prior to restoration, and therefore requires two additional assumptions: (1) similar pre-restoration avifaunal composition among restoration sites and (2) restoration sites have experienced similar post-restoration disturbance regimes (e.g. climate and grazing). We attempted to account for pre-restoration avifaunal composition by including pre-restoration RDV cover and climatological variables in the model. The climatological variables also helped to control for post-restoration climatic differences among restoration. The inclusion of a random effect for site also helped us to meet these assumptions, although as discussed above, grazing after restoration was variable among the sites in our study.

In conclusion, pond-and-plug and other partial channel fill techniques improve habitat for birds in riparian montane meadows, but responses were evident in only half the bird species we assessed. Increased planting densities at the time of restoration would likely accelerate and enhance outcomes for birds, as would prioritizing restoration in geographies where focal species tend to occur in higher abundance or are most likely to colonize. The results of our study likely apply to other forms of hydrologic restoration techniques in montane riparian meadows that achieve similar post-restoration conditions (e.g. elevated dry-season water table, increased floodplain inundation, and increased RDV), but additional evaluations of specific techniques are warranted. Continued monitoring is needed to inform adaptive management that ensures restoration projects deliver the best possible results for the investment.

Acknowledgments

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Restoration sites where we studied bird response to montane riparian meadow restoration in California.

Table S2. Descriptive statistics (mean [min–max]) for habitat variables.

Table S3. Parameter estimate and standard error (SE) for the effect of shrub cover.

Figure S1. Mean predictions and ±95% CI for the marginal effect of the pre-restoration percent cover.

Figure S2. Mean predictions and ±95% CI for the marginal effect of stream flow on abundance.

Figure S3. Mean predictions and ±95% CI for the marginal effect of precipitation on abundance.

Figure S4. Mean predictions and ±95% CI for the marginal effect of temperature on abundance.