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Low flows in a regulated river system are associated with reduced breeding bird abundance and diversity in Yosemite National Park, California

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Abstract

River regulation can alter the magnitude, frequency, duration, and timing of flows, which influences the function of downstream ecosystems. Bird communities can be useful indicators of ecosystem function as individual species respond to varied changes in habitat structure and food availability. We examined the relative importance of different aspects of a regulated flow regime (average daily flow, the number of days flows fell below the 25th percentile, the timing and magnitude of maximum flows, and the inter-annual duration of flows below the historical median) on predicted bird abundance and diversity using 11 years of data collected within a floodplain meadow system located downstream of Hetch Hetchy Reservoir in Yosemite National Park, California. We found that prolonged periods of low flows were negatively associated with the number of breeding birds detected, as well as the species richness of the breeding bird community. Species richness was also negatively correlated with delays in spring runoff delivery. We opportunistically looked at the same hydrologic variables in a parallel unregulated system, the Merced River through Yosemite Valley, and did not find the same strong relationship with bird community data. This suggests that the dam may be exacerbating the effects of drought.

KEYWORDS
breeding birds, drought, ecosystem function, Hetch Hetchy Reservoir, riparian ecosystem, river regulation, Yosemite

1 | INTRODUCTION

Regulation of rivers by dams can drastically reduce annual discharge and alter the natural timing of floods, thereby negatively affecting downstream riparian ecosystems (Bunn & Arthington, 2002; Kingsford, 2001; Poff et al., 1997). Despite representing a small fraction of total land cover, riparian ecosystems, including riparian habitat adjacent to rivers, harbor a disproportionately high number of species (Gregory, Swanson, McKee, & Cummins, 1991; Knopf, Johnson, Rich, Samson, & Szaro, 1988). Thus, dams contribute substantially to the decline of many species, including those of conservation interest such as threatened and endangered species (Losos, Hayes, Phillips, Wilcove, & Alkire, 1995). This underscores the need to understand complex and varied ecological responses to river regulation in order to inform dam management to reduce negative impacts on wildlife and benefit downstream ecosystems (Chen & Olden, 2017).

Birds are often used as indicators of intact ecosystem processes due to their varied nesting, foraging, and sheltering requirements, a rich body of literature covering their natural history, and their ease of survey by skilled observers (Canterbury, Martin, Petit, Petit, &

Bradford, 2000; Hutto, 1998). Birds that depend on riparian riverine habitats are particularly good indicators of river processes, as their distribution, abundance, diversity, persistence (Chiu, Kuo, Hong, & Sun, 2013; Hinojosa-Huerta, Nagler, Carillo-Guererro, & Glenn, 2013; Reiley, Benson, & Bednarz, 2013; Royan et al., 2015; Royan, Hannah, Reynolds, Noble, & Sadler, 2013), breeding timing (Arthur et al., 2012; Strasevicius, Jonsson, Erik, Nyholm, & Malmqvist, 2013), and breeding success (Cain, Morrison, & Bombay, 2003; Hoover, 2006; Picman, Milks, & Leptich, 1993; van Oort, Green, Hepp, & Cooper, 2015) are all linked to the timing and magnitude of both high and low flows.

River discharge influences the availability and quality of food for birds (Table A1). For example, altered flow regimes can result in decreased availability of emergent aquatic insect prey for birds (Poff & Zimmerman, 2010; Strasevicius et al., 2013) resulting from mismatches in timing of insect reproduction or maturation with historically predictable floods (Lytle & Poff, 2004). During the breeding season, many birds rely heavily on invertebrate prey, including terrestrial invertebrates and emergent aquatic insects, to meet their energetic and nutritional needs, as well as the needs of their rapidly growing young (Martin, 1995; Trevelline et al., 2018). Some riparian birds derive more than half of their energetic needs from aquatic food chains, and this percentage can increase in dry years (B. K. Jackson et al., 2020). Additionally, altered flow regimes that result in reduced water availability can promote differential investment in plant growth (e.g., investment in roots at the expense of fruits and seeds), that reduces plant food availability to birds directly, as well as indirectly through reductions in food to invertebrate herbivores, the invertebrate predators that prey on them, and ultimately breeding birds (Bazzaz, Chiariello, Coley, & Pitelka, 1987; Eziz et al., 2017; Rai et al., 2018).

Altered flow regimes due to river regulation have the potential to change physical structure and suitability of bird habitat. Reduced water availability and altered flood timing can decrease the amount and variety of physical plant structure available to birds for sheltering, foraging, and nesting (Bazzaz et al., 1987; Eziz et al., 2017). Hydrologic changes that simplify habitat structure may result in a reduction in bird species richness (Dobson, La Sorte, Manne, & Hawkins, 2015; MacArthur & MacArthur, 1961; Mills, Dunning, & Bates, 1991). For example, low baseflow conditions, often associated with regulated rivers, inhibit long-term cottonwood (*Populus* sp.) and willow (*Salix* sp.) recruitment (Rood et al., 2003), both of which provide riparian nesting habitat. Furthermore, regulated river flows often favor more homogeneous and late-successional vegetation by reducing the duration and extent of wetland inundation, allow woody plant recruitment in the stream channel, and reduce annual growth of riparian plants (Auble, Friedman, & Scott, 1994; Graf, 2006; Gregory et al., 1991; Harris et al., 1987; Poff & Zimmerman, 2010; Stromberg & Patten, 1990). Finally, floods that are asynchronous with riparian bird life cycles can result in direct mortality or nest failure due to inundation (B. T. Brown & Johnson, 1985).

Despite the recognition that regulated river hydrology has a large impact on the structure of riparian habitat (Poff et al., 1997) and the timing and magnitude of aquatic prey available to breeding birds (Kennedy et al., 2016; Robinson, Uehlinger, & Monaghan, 2003), relatively few studies have examined the influence of regulated river hydrology on abundance and diversity of breeding birds compared to studies of aquatic organisms. Bird communities should respond to multiple aspects of the flow regime that may be confounded (Poff & Zimmerman, 2010). Investigation of the relative influence of various aspects of the flow regime on bird community composition has potential to inform the design of water releases aimed at mitigating the impact of regulated river hydrology on the downstream riparian ecosystem. In this study we explored the relationship between characteristics of regulated river hydrology and breeding bird community metrics downstream of Hetch Hetchy Reservoir in Yosemite National Park, California with 11 years of bird survey data. We examined how flood frequency, timing, and duration, as well as annual flow magnitude, predicted avian species richness, overall abundance, and the abundance of a suite of riparian focal species with varied nesting and foraging habits representing the predominant habits of avian species in the study area (sensu Ralph, Geupel, Pyle, Martin, & DeSante, 1993). We then assessed how the same aspects of the flow regime predicted the same bird community metrics over seven coincident years along an unregulated section of an adjacent drainage, the Merced River in Yosemite Valley. This opportunistic comparison allowed us to assess how changes in breeding bird community metrics might be explained by the influence of regulated river hydrology.

2 | FIELD METHODS

2.1 | Study system

We conducted our study in adjacent watersheds in Yosemite National Park (Figure 1a). These watersheds are comparable in size, elevation, aspect, and climate. Both rivers support similar vegetation communities and have similar channel morphology and bed composition. The Tuolumne River is dammed by O'Shaughnessy Dam to form Hetch Hetchy Reservoir and represents a regulated system. Operation of the dam has altered aspects of the flow regime downstream: annual peak discharge has been reduced by 35%; the duration of high flow periods have been reduced by 40%; and average monthly discharge has been reduced by 65% (Russo, Fisher, & Roche, 2012). We collected regulated system breeding bird community data in Poopenaut Valley, which covers an area of approximately 0.25 km^2 and is situated 4 km downstream of the reservoir (Figure 1b). Despite its relatively small size, Poopenaut Valley is comprised of a variety of habitats, such as an ephemeral pond, mixed conifer forest, montane meadow, and riparian cottonwood, alder, and willow. In comparison, the Merced River flows freely through Yosemite Valley and represents an unregulated system. Yosemite Valley is larger than Poopenaut Valley, and the Merced River in Yosemite Valley is affected by rip-rap, bridges, roads, and other development. We controlled for the difference in size and physical characteristics between these study areas by collecting breeding bird community data at sub-locations in Yosemite Valley with similar habitat elements to that of Poopenaut Valley, further described below (Figure 1c).

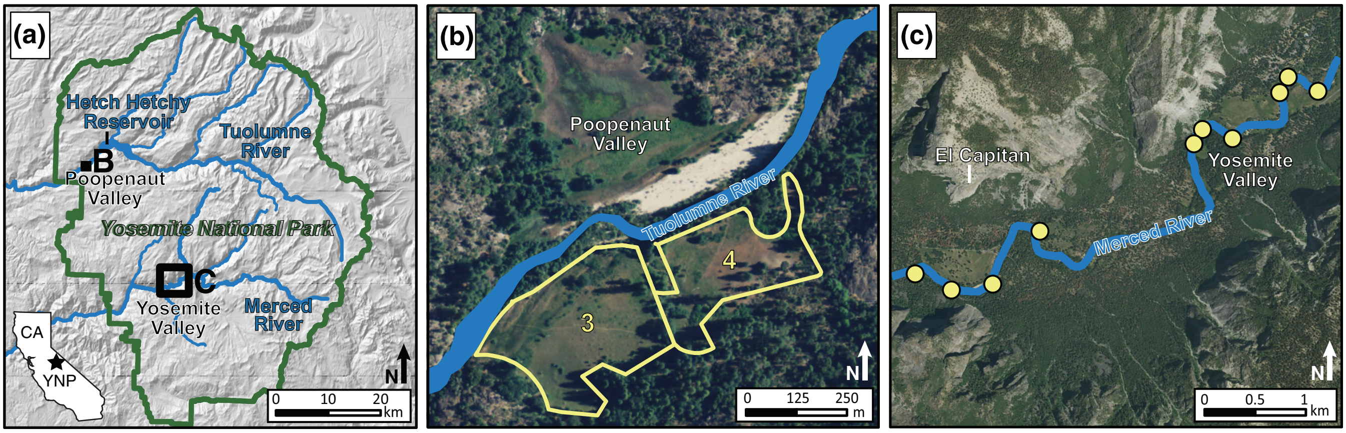

FIGURE 1 (a) Location of the Tuolumne River, Poopenaut Valley, the Merced River, and Yosemite Valley in Yosemite National Park, California. (b) Bird area search locations, outlined in yellow, in the regulated system of Poopenaut Valley. (c) Bird point count locations included in our analysis, yellow points, in the unregulated system of Yosemite Valley along the Merced River [Color figure can be viewed at wileyonlinelibrary.com]

2.2 | Bird surveys

We conducted 11 years (2007–2017) of standardized area search surveys in Poopenaut Valley, our regulated system. We chose the area search method for characterizing the bird community in Poopenaut Valley because of the study area's small size (Ralph et al., 1993). Area search surveys were performed on two plots 0.4 and 0.03 km^2 in size (areas three and four respectively; Figure 1b). Plots were designated so that a single observer could survey each area in 20 min between dawn and 10 a.m. (Ralph et al., 1993). We conducted surveys during the peak of the bird breeding season (May 15–June 30) on three separate occasions each season, with visits occurring at least 10 days apart. During area searches, the observer recorded the species and number of all birds seen or heard within a plot. Birds observed within 10 m of the plot's edge were included, except for the shared boundary between the two plots. The surveyor recorded the method of detection (either visual or aural) along with any observations that indicated breeding status including singing, territorial behaviors, carrying nesting material or food, copulation, and the presence of a nest, eggs, or dependent young from that year.

We conducted point count surveys in our unregulated system as part of a separate long-term monitoring effort in seven (2011–2017) out of the 11 years we surveyed the regulated system. For point count surveys the observer stood at a point and recorded the species, number, and distance to all birds seen or heard in 7 min (Siegel, Wilkerson, & Goldin Rose, 2010). The 10 points included in this analysis are a subset of all points surveyed. Selected points were all those that had similar microhabitat to that found in Poopenaut Valley (within 75 m of wet meadow and riparian edge habitat; Figure 1c). In addition, to sample a land area comparable to the area search plots in our regulated system we limited the survey data to birds detected within a 100 m radius of the survey point. Data quality between surveyors (the same surveyor within a year for both systems) was maintained by a rigorous hiring process and annual training.

The juxtaposition of these two systems was not part of an initial study design, and our field methods for measuring breeding bird community data differs. Area searches are thought to be better than point counts at detecting less common and/or cryptic species (Loyn, 1986). Therefore, we may have an increased ability to detect subtle changes in bird response in the unregulated as compared to the regulated system. However, we believe that the potential impacts of different field methodology on our conclusions are limited given that any additional bird abundance attributable to harder to detect species would be relatively small compared to other species regularly detected, we worked to minimize physical differences in site characteristics between the two systems as described above, point counts over multiple stations, as in our study, can provide reasonable estimates for more intensive survey methods of avian abundance, such as area searches or spot mapping (Toms, Schmiegelow, Hannon, & Villard, 2006), and our use of focal species, described below, allows us to draw conclusions about habitat suitability for a wide variety of birds, including potentially undetected species. Our comparison is opportunistic, but worth considering, as both methods of bird survey are well-established methods to measure changes in bird community composition over time and space (Ralph et al., 1993), and most importantly, our goal was to measure the response of the bird community to hydrology metrics within systems, rather than directly compare bird community metrics between systems.

We included all detected bird species in our analyses, and additionally selected five bird species as riparian focal species. Selecting a suite of focal species with varied foraging and nesting requirements provides a holistic view of what benefits the riparian ecosystem. Focal species included warbling vireo (*Vireo gilvus*), yellow warbler (*Setophaga petechia*), song sparrow (*Melospiza melodia*), black-headed grosbeak (*Pheucticus melanocephalus*), and western wood-pewee (*Contopus sordidulus*; Table 1). All focal species are closely associated with riparian habitat, and represent diverse life histories. Four of the species are identified as important indicators and thus focal species in

TABLE 1 Focal riparian bird species and their life history characteristics

Species	Neotropical migrant	Nest	Foraging behavior and diet
Western wood-pewee (*Contopus sordidulus*)	Yes	Cup nest usually located on/at a fork in a branch near ground or up to over 25 m in height	Hawking insectivore
Warbling vireo (*Vireo gilvus*)	Yes	Hanging cup nest generally in deciduous tree or shrub typically placed higher than 3 m	Foliage-gleaning insectivore
Yellow warbler (*Setophaga petechia*)	Yes	Cup nest in tree, sapling or shrub, typically placed lower than 3 m	Foliage-gleaning insectivore
Song sparrow (*Melospiza melodia*)	No	Cup nest generally located deep in supporting plant, typically lower than 3 m	Ground and foliage gleaning omnivore
Black-headed grosbeak (*Pheucticus melanocephalus*)	Yes	Cup nest typically placed in outer branches of deciduous tree or bush, typically lower than 3 m	Foliage gleaning omnivore

Note: Data compiled from Arcese, Sogge, Marr, and Patten (2002), Bemis and Rising (2020), Bryce (2006), Gardali and Ballard (2020), Lowther, Celada, Klein, Rimmer, and Spector (2020), and Ortega and Hill (2022).

a riparian conservation plan developed by a regional partnership (Riparian Habitat Joint Venture [RHJV], 2004). The fifth species, Western wood-pewee, was included to represent a common foraging strategy not typically employed by the other four species.

3 | ANALYTICAL METHODS

We calculated abundance of all bird species, abundance of riparian focal species, and overall species richness for both area search and point count surveys annually. We lumped data in the regulated system due to non-independence due to a shared border between the two plots (Figure 1b). We calculated abundance and focal abundance by finding the greatest number of individuals detected by species over three annual visits, summing those counts, and averaging over sample points by year where appropriate (i.e., the unregulated system point count stations). We calculated species richness as the number of unique species detected in the study area over three annual visits (regulated system), or the number of unique species detected at each point count station over three visits, averaged over all points sampled by year (unregulated system).

We chose five independent variables that are linked to resources birds need for breeding and survival, and that tend to be altered by river regulation (Poff et al., 1997) to represent the flow regime (Table A1). These variables were: (a) average daily flow (average of the daily average flow, calculated by water year), (b) the number of days with flow below the 25th percentile, (c) Julian date of the maximum flow (measured as the highest daily average between January 1 and June 30 in order to encompass dates immediately preceding and during the avian breeding season), (d) volume of the instantaneous maximum flow, and (e) the number of years since median daily flow was at or above the historic median, or "years since median." We calculated the historic median as the median daily flow recorded between 1968, when the present water diversion structures from the dam were completed, and 2017 when our study was complete. We calculated percentiles using the same time period. We retrieved river discharge data from the US Geological Survey (USGS) (http://nwis.waterdata.usgs.gov/nwis/rt). For the regulated site, we used hydrologic data collected over the water years of 2007 through 2017 from the Tuolumne River at Hetch Hetchy gage (gage id: 11276500). For the unregulated sites, we used data collected from the Merced River at Happy Isles Bridge gauge (gage id: 11264500). The California water year is October 1 to September 30. We also included years since fire as a variable in the model selection process in order to control for the effects of the Rim Fire which burned our regulated study area in August 2013.

We assessed which of our chosen hydrologic variables best predicted each of the three bird response metrics (overall breeding bird abundance, the abundance of riparian focal species, and overall species richness) separately using an information-theoretic model selection approach based on Akaike's information criterion (AIC; Anderson & Burnham, 2002; Burnham & Anderson, 2004). Analyses were performed in R version 4.1.3 (R Core Team, 2022). We assessed collinearity among independent variables with a correlation matrix and variance inflation factors (VIF) in R software package *car* using *cor* and *vif* functions respectively (Fox & Weisberg, 2019). We considered correlations of greater than 0.7, and VIF values greater than 5 within a model containing all covariates as excessively collinear (Heiberger & Holland, 2004). Given fewer years of data for the unregulated study site in Yosemite Valley (7 years) compared to the regulated study site in Poopenaut Valley (11 years) we needed to reduce the number of predictors in our unregulated system model selection. We chose to drop instantaneous maximum flow from the unregulated analysis because we felt that the role this variable plays in determining habitat quality for birds in the unregulated system is partially captured in average daily flow, and less subject to large variation from the historical norm than in the regulated system. We assessed global models for the assumptions of linear models. No transformations were needed. We compared competing models with a model selection table made with the *dredge* function in R package *MuMIn* (Bartoń, 2022). The null model (i.e., intercept only) was included in each of the sets of competing models for comparative purposes. We ranked each competing model using AIC corrected for small sample size (AIC_c; Anderson &

Burnham, 2002); and considered ΔAIC_c values within four units of the top model as worth presentation (Burnham & Anderson, 2004). We used Akaike weights (ω_i) to determine the relative support a model received among all of the candidate models in the set. In all of our statistical tests, we considered results significant at the $\alpha = .05$ level.

4 | RESULTS

In the regulated system of Poopenaut Valley between 2007 and 2017, we made 1,322 detections of 63 species while conducting area search surveys (Table A2). Across plots, the five most frequently detected birds in descending order were black-headed grosbeak, spotted towhee (*Pipilo maculatus*), western wood-pewee, American robin (*Turdus migratorius*), and warbling vireo.

Overall abundance in the regulated system was best predicted by a bivariate model including number of days that flow was below the 25th percentile and the average daily flow (Table 2). Abundance was negatively correlated with number of days below the 25th percentile and positively correlated with average daily flow (Figure 2). No other models were within four AIC_c units of the best model.

Abundance of riparian focal species in the regulated system was best predicted by a bivariate model including number of days below the 25th percentile and average daily flow (Table 2). Abundance of riparian focal species was negatively correlated with number of days below the 25th percentile, and positively correlated with average daily flow (Figure 3). Univariate models including these two predictor variables were also supported (Table 2). Three additional bivariate models were supported: (a) Average daily flow and years since fire, (b) average daily flow and Julian date of peak flow, and (c) average

TABLE 2 Retained regression models ($\Delta AIC_c \leq 4$) for predicting avian community metrics calculated from area search surveys in the regulated system, the Tuolumne River in Poopenaut Valley, between 2007 and 2017, and from point count surveys in the unregulated system, The Merced River in Yosemite Valley, between 2011 and 2017, with corresponding Akaike information criterion for small sample size (AIC_c) scores, Akaike weights (ω_i) and variation explained (Adj R^2)

	AIC_c	ΔAIC_c	ω_i	Adj R^2
Regulated system—Poopenaut Valley				
Abundance				
Days below the 25th percentile (−) and average daily flow (+)	70.78	0	0.75	0.97
Null	103.33	32.55	<0.01	—
Abundance of riparian focal species				
Days below the 25th percentile (−) and average daily flow (+)	68.01	0	0.26	0.73
Average daily flow (+)	68.29	0.28	0.23	0.60
Days below the 25th percentile (−)	69.75	1.75	0.11	0.54
Average daily flow (+) and years since fire (+)	70.92	2.92	0.06	0.64
Average daily flow (+) and Julian date of maximum flow (−)	70.96	2.95	0.06	0.64
Average daily flow (+) and years since median flow (−)	71.04	3.04	0.06	0.64
Null	75.57	7.56	0.01	—
Species richness				
Days below the 25th percentile (−) and Julian date of maximum flow (−)	52.70	0	0.58	0.89
Maximum instantaneous flow (−), years since fire (+), and years since median flow (−)	55.84	3.14	0.12	0.92
Null	70.53	17.84	<0.01	—
Unregulated system—Yosemite Valley				
Abundance				
Null	49.41	0	0.73	—
Days below the 25th percentile (−)	53.00	3.59	0.12	0.26
Abundance of riparian focal species				
Null	31.53	0	0.58	—
Days below the 25th percentile (−)	33.82	2.29	0.18	0.39
Years since median flow (−)	35.26	3.73	0.09	0.25
Julian date of maximum flow (+)	35.51	3.98	0.08	0.22
Species richness				
Null	31.52	0	0.84	—

Note: Null models (i.e., intercept only) are also included. Signs in parentheses indicate the direction of the relationship between predictor and response variables.

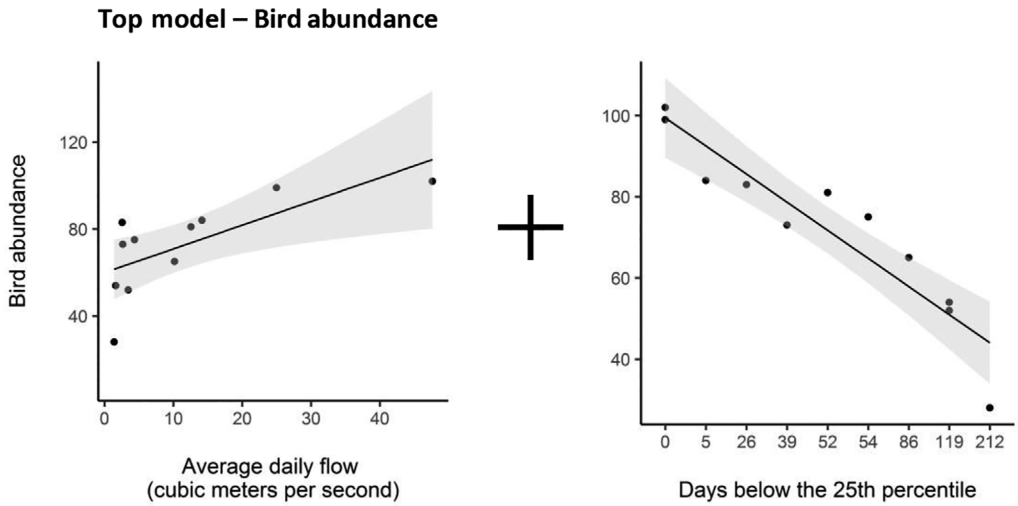

FIGURE 2 The best supported model predicting abundance in Poopenaut Valley, the regulated system. Abundance was best predicted by a bivariate model including average daily flow and the number of days in a water year average daily flow was below the 25th percentile. The shaded areas represent 95% confidence intervals

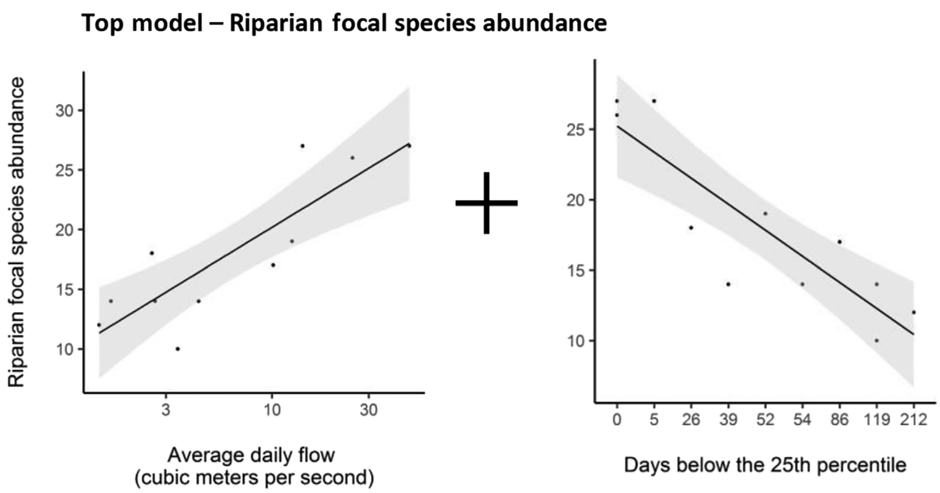

FIGURE 3 The best supported model predicting focal species abundance in Poopenaut Valley, the regulated system. Riparian focal species abundance (warbling vireo, black-headed grosbeak, western wood-pewee, song sparrow, and yellow warbler, clockwise from top left, then center), was best predicted by a bivariate model including the average daily flow and the number of days in a water year average daily flow was below the 25th percentile. The shaded areas represent 95% confidence intervals

daily flow and years since median flow. In these models, abundance of riparian focal species was positively correlated with average daily flow, positively correlated with years since fire, and negatively correlated with Julian date of peak flow and years since median flow (Table 2). No other models were within four AIC_c units of the best model.

Species richness in the regulated system was best predicted by a bivariate model including number of days below the 25th percentile and Julian date of peak flow (Table 2). Species richness was negatively correlated with both predictor variables (Figure 4). A second model containing instantaneous maximum flow, years since fire, and years since median flow was also supported. Species richness was positively correlated with years since fire, and negatively correlated with maximum instantaneous flow and years since median flow (Table 2). No other models were within four AIC_c units of the best model.

In the unregulated system of Yosemite Valley between 2011 and 2017, we made 2,637 detections of 67 species while conducting point counts (Table A2). The five most common species, in descending order, were song sparrow, warbling vireo, brewer's blackbird (*Euphagus cyanocephalus*), western wood-pewee, and black-headed grosbeak.

We did not find evidence of a strong correlation between our chosen hydrologic variables and bird response metrics in the unregulated system. In all cases, the null model was the best supported model, indicating other unmeasured variables may be more important in determining bird community metrics (Table 2).

5 | DISCUSSION

The results of our study provide preliminary evidence that low flows associated with river regulation may compound the effects of drought on breeding birds. We captured the full range of hydrologic conditions during our study period, including multi-year drought, average, and above average water years. The state of California and our study system experienced an historic drought between the water years of 2012 and 2016. Intra-annual drought and seasonal low flows are

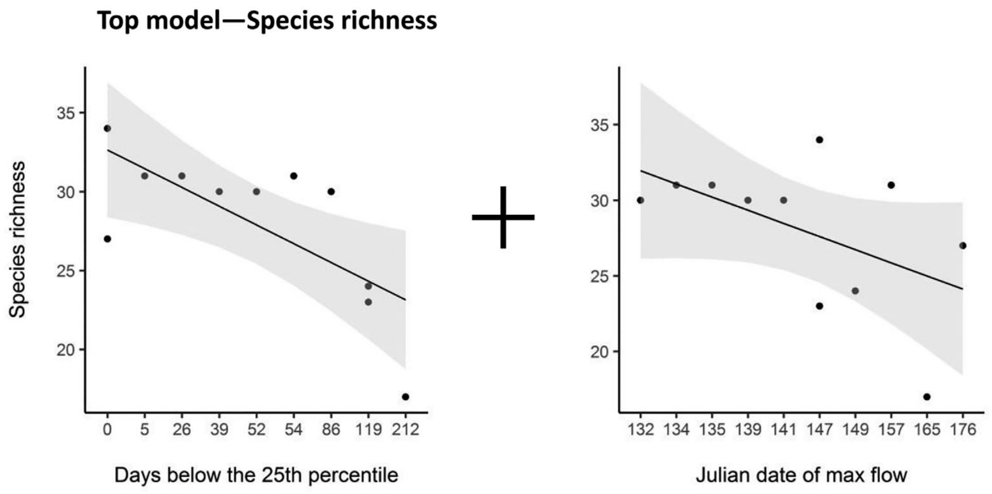

FIGURE 4 The best supported model predicting species richness in Poopenaut Valley, the regulated system. Species richness was best predicted by a bivariate model including the number of days in a water year average daily flow was below the 25th percentile and the Julian date of the maximum flow. The shaded areas represent 95% confidence intervals

common disturbances in our study system (Gasith & Resh, 1999), and riparian organisms living in systems like ours often exhibit life-history traits that allow them to be resistant or resilient to drought (Bunn & Arthington, 2002; Lytle & Poff, 2004). Therefore, bird responses to drought may be delayed (Hinojosa-Huerta et al., 2013) unless other pressures are present (Fausch, Baxter, & Murakami, 2010; M. C. Jackson, Loewen, Vinebrooke, & Chimimba, 2016). Dams may provide this additional pressure as they can create conditions downstream that mimic permanent drought, and reduce overall annual discharge (Lake, 2003; Russo et al., 2012). In our study, breeding bird diversity and abundance decreased in response to both intra-annual (i.e., average daily flow and number of days flow was below the 25th percentile) and to inter-annual low flows (i.e., years since median flow) in our regulated system (Table 2, Figures 2–4).

The influence of river regulation on Poopenaut Valley below O'Shaughnessy Dam can perhaps be best seen in a comparison of the observed flow and a modeled unimpaired estimate of flow if the dam were not present (Lundquist et al., 2016; Figure 5). In the extended drought of 2013, 2014, and 2015 the shape of the observed hydrograph below the dam is dramatically different than the shape of the estimated unimpaired flow (Figure 5) and the shape of the observed flow in Yosemite Valley (Figure 6); In these years a spring snowmelt peak appears delayed, reduced, and somewhat smoothed out in the regulated system. In contrast, even with multi-year drought the estimated unimpaired flow in the regulated system and the observed flow in the unregulated system show pronounced spring snowmelt peaks, and fewer days at or below the 25th percentile. All three of our bird metrics appear to decrease during these drought years in the regulated system (Figure 5), but this pattern does not appear as pronounced in the unregulated system (Figure 6). We suggest that the presence of spring snowmelt peaks within historical norms of timing and magnitude, and resilience to low-flow conditions due to the absence of chronic reductions characteristic of a regulated system (Russo et al., 2012) kept the deleterious impacts of multi-year drought from having as strong or immediate an impact in the unregulated system.

O'Shaughnessy Dam reduces water delivery to the ecosystem of Poopenaut Valley (Russo et al., 2012), and in drought years this reduction may be especially detrimental. Water reduction due to drought and/or river regulation is negatively associated with floodplain wetland maintenance (Kingsford, Basset, & Jackson, 2016; Vivian, Godfree, Coloff, Mayence, & Marshall, 2014), riparian vegetation survival and recruitment (Harris et al., 1987; Rood et al., 2003), and the maintenance of invertebrate communities (Dewson et al., 2007; Holmquist & Schmidt-Gengenbach, 2012; Holmquist & Waddle, 2013; Jansson, Nilsson, Dynesius, & Andersson, 2000; Kingsford, 2001; Stromberg, 1993, 2001; Stromberg, Beauchamp, Dixon, Lite, & Paradzick, 2007). Riparian bird communities are shaped by these processes as they provide food resources, nesting sites, and shelter (Albright et al., 2010; Hinojosa-Huerta, 2006; Hinojosa-Huerta et al., 2013; Hinojosa-Huerta, Iturribarria-Rojas, Zamora-Hernandez, & Calvo-Fonseca, 2008). We observed lower overall breeding bird abundance and abundance of riparian focal species in the regulated system in years when average daily flow was reduced and days where flow remained below the 25th percentile increased (Table 2). We observed reduced species richness in years where days that flow was below the 25th percentile increased, as well as when the Julian date of peak flow was later in the year. We discuss the specific mechanisms that may be contributing to our observed patterns below.

In a separate study, we found that birds in our study areas rely heavily on an aquatic-derived food chain (B. K. Jackson et al., 2020), and when food quantity or quality is reduced, birds will breed at lower densities (Rolando, Caprio, Rinaldi, & Ellena, 2007). Breeding birds rely heavily on invertebrate prey (Martin, 1995; Trevelline et al., 2018), and aquatic insect emergence is often highest in the spring when terrestrial invertebrate prey availability is low (Nakano & Murakami, 2001). It follows then that processes that impact the emergent aquatic insect community will have an impact on the breeding bird community. The availability and quality of emergent aquatic insect prey is impacted by low flows due to river regulation and/or drought in several ways. Within the river channel low flows (captured in our analysis by average daily flow and days below the 25th percentile) can result in decreased water velocity and depth, increased sedimentation, changes to nutrient concentrations, changes in water temperatures, reduced dissolved oxygen levels, a reduction in wetted area, or a loss of connectivity between wetted patches including the

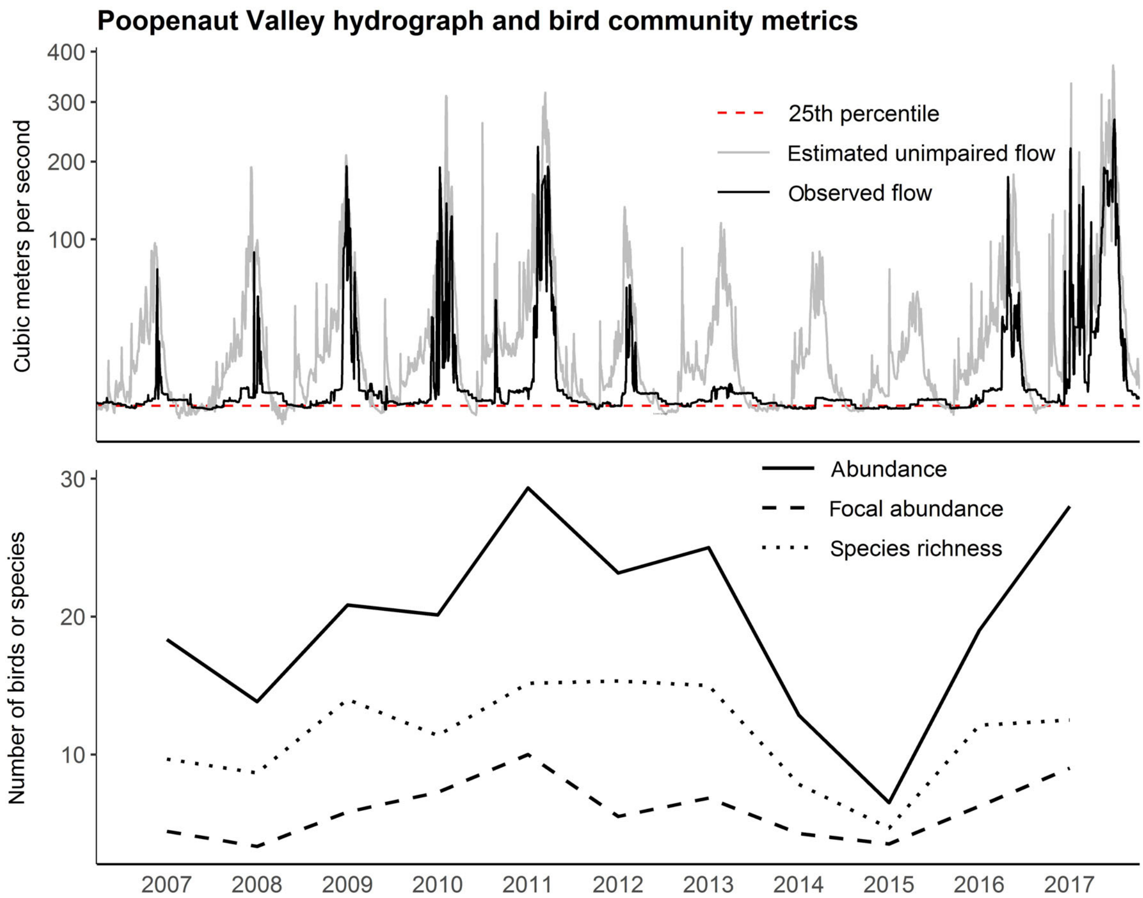

FIGURE 5 The hydrograph of the Tuolumne River through Poopenaut Valley compared chronologically with bird community metrics. Flow is the volume of water in cubic meters per second as recorded by the Tuolumne River at Hetch Hetchy US Geological Survey gage, upstream of Poopenaut Valley (gage id: 11276500). Estimated unimpaired flow is the modeled volume of water that would flow through Poopenaut Valley if O'Shaughnessy Dam and Hetch Hetchy Reservoir were not present (Lundquist et al., 2016). The 25th percentile line is calculated from observed flows recorded between 1968, when the present water diversion structures from the dam were completed, and 2017 when our study was complete. Focal abundance is the abundance of our riparian focal species including song sparrow, yellow warbler, western wood-pewee, black-headed grosbeak, and warbling vireo. No error bars are appropriate as data were analyzed as a single replicate [Color figure can be viewed at wileyonlinelibrary.com]

hyporheic zone (Boulton, 2003; Dewson et al., 2007; Holmquist & Waddle, 2013; Lake, 2003; Russo et al., 2012). The interaction of these factors is associated with changes in taxonomic composition, including reductions in diversity of emergent aquatic insects, decreased magnitude of emergence, and changes in emergence timing (Dewson et al., 2007; Holmquist et al., 2011; Holmquist & Schmidt-Gengenbach, 2012; Holmquist & Waddle, 2013; Rader & Belish, 1999). In general, river regulation is associated with a reduction in biomass, quantity, and quality of emergent aquatic insect prey (Carey, 2009; Gratton & Zanden, 2009; Jonsson, Deleu, & Malmqvist, 2013). The above factors likely contribute to our observed reductions in focal species abundance and overall abundance associated with reduced flow in this study.

Another large portion of breeding birds' diets is likely largely made up of terrestrial invertebrates (Martin, 1995; Trevelline et al., 2018). Systematic and long-lasting reductions in flow due to river regulation and/or drought impact invertebrates immediately adjacent and connected to the river channel in a number of ways. In the short term, inadequate inundation of floodplain wetlands reduces available habitat for invertebrates that feed and take shelter in inundated riparian vegetation (Holmquist & Schmidt-Gengenbach, 2012; Ormerod, Wade, & Gee, 1987; Wright, Blackburn, Clarke, & Furse, 1994). Low flows also reduce primary productivity and species richness of the riparian plant community (Harris et al., 1987; Jansson et al., 2000; Rai et al., 2018; Stromberg, 2001), resulting in decreased terrestrial invertebrate diversity and abundance (V. K. Brown, 1984; Knops et al., 1999; McCluney & Sabo, 2012; Schaffers, Raemakers, Sykora, & ter Braak, 2008). Conversely, higher plant moisture levels when water is not limited contributes positively to terrestrial invertebrate community composition and biomass by providing a refuge from desiccation, a humid microclimate, and a source of water for direct ingestion (Wenninger & Inouye, 2008). Terrestrial invertebrates also feed on emergent aquatic insects (Marczak, Thompson, & Richardson, 2007), and processes that impact the aquatic invertebrate community as outlined above are associated with decreased biomass of terrestrial invertebrates (Benke, 2001; Jonsson et al., 2013).

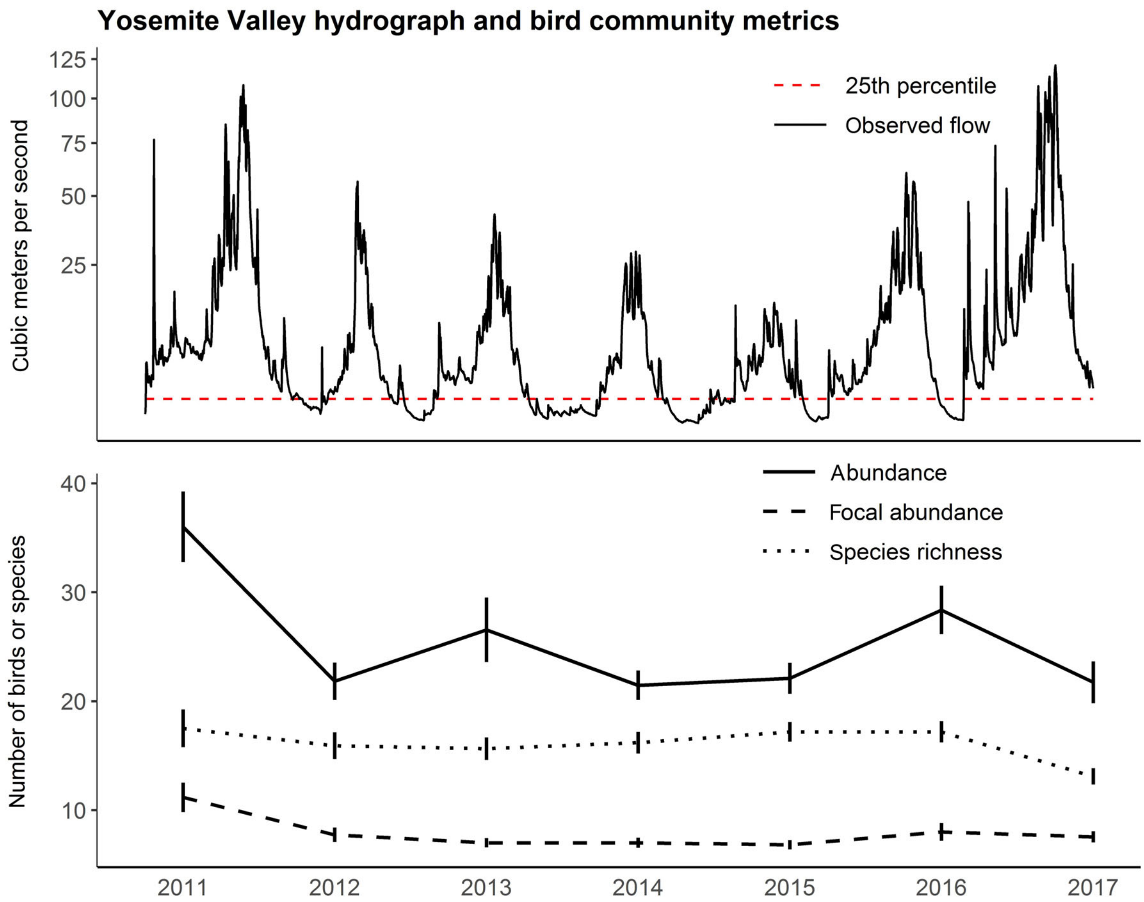

FIGURE 6 The hydrograph of the Merced River through Yosemite Valley compared chronologically with bird community metrics. Flow is the volume of water in cubic meters per second as recorded by the Merced River at Happy Isles Bridge US Geological Survey gage (gage id: 11264500). We used the same period of time to calculate the 25th percentile in Yosemite Valley as in Poopenaut Valley: flows between 1968, when the present water diversion structures from O'Shaughnessy Dam were completed, and 2017 when our study was complete. Focal abundance is the abundance of our riparian focal species including song sparrow, yellow warbler, western wood-pewee, black-headed grosbeak, and warbling vireo, as measured at 10 point count stations in Yosemite Valley. Error bars represent *SEM* [Color figure can be viewed at wileyonlinelibrary.com]

Nesting sites and shelter are provided by riparian vegetation in both the regulated and unregulated systems in our study. In the long term, low flows due to river regulation in the Sierra Nevada can result in a loss of riparian obligate shrubs, and a shift to more upland associated species (Harris et al., 1987), and regulated rivers generally exhibit reduced plant species richness and cover as compared to unregulated rivers (Jansson et al., 2000), which is problematic as bird community composition is tied to plant community composition (Hinojosa-Huerta et al., 2008; Lynn, Morrison, Kuenzi, Neale, & Sacks, 1998; Narango, Tallamy, & Marra, 2018; Rotenberry, 1985). In the short term, birds may depend on overbank flooding during the breeding season to create standing water under nests which reduces predator access, provides greater nest concealment, and increases breeding success (Cain et al., 2003; Caldwell et al., 2013; Hoover, 2006; Lima, 2009; Picman et al., 1993) Additionally, volume of aboveground vegetative biomass is influenced by water availability (Eziz et al., 2017), which is positively associated with high quality bird habitat (Hinojosa-Huerta et al., 2008), as bird density can be proportional to vegetation density (Mills et al., 1991), and species richness of birds can be positively correlated with three-dimensional complexity of vegetation structure (Dobson et al., 2015; MacArthur & MacArthur, 1961).

We observed a reduction in species richness when the Julian date of maximum flow occurred later in the growing season in the regulated system (Table 2, Figure 4). In eight out 11 years we collected data in the regulated system the Julian date of maximum flow was later than when the unimpaired estimate placed it (Lundquist et al., 2016). When later, peak flow was on average 30 ± 49 (*SD*) days later than the unimpaired estimate (range 1–148 days later). The timing of peak flows is known to be a determinant of habitat availability and suitability for breeding birds (Lima, 2009; Royan et al., 2013), as well as a factor influencing invertebrate prey community composition (Brittain & Eikeland, 1988). We believe that the delay in water delivery and overbank flooding at appropriate times for biomass production in the vegetative community may be more influential to the observed patterns in species richness than direct loss of nests due to delays in peak flows.

6 | MANAGEMENT IMPLICATIONS

In California alone, riparian habitat is estimated at approximately 15% of previous extent 150 years ago (RHJV, 2004). Habitat loss and alteration is cited as a leading cause of continent-wide bird declines since 1970 (Rosenberg et al., 2019). These facts underscore the need for adaptive river management for birds and the ecosystem processes on which they depend.

In general, the avian community of Poopenaut Valley will benefit from keeping flows sufficiently high (i.e., overbank wetland inundation) during the plant growing and bird breeding season to (a) prevent nest building in the stream channel at heights vulnerable to inundation, (b) support invertebrate and vegetative plant biomass that serves as food, shelter, and nest sites for birds on an annual basis (Eziz et al., 2017; Holmquist & Schmidt-Gengenbach, 2012; Kingsford et al., 2016; Rai et al., 2018; Vivian et al., 2014), as well as preventing conifer encroachment supra-annually (Lubetkin et al., 2017), and (c) support willow recruitment with sufficient late-summer flow (Lynn et al., 1998; Rood et al., 2003). Opportunistic nest monitoring, a separate component of the larger study not presented here, suggests that the timing of maximum flow over the study period appears to be contributing to the first goal, but deviation from the natural timing of maximum releases, specifically delays, are likely contributing to reduced species diversity. The results of this study suggest that the second goal is being met in wetter years, but managers are falling short in multi-year droughts. We found that reductions in flow, especially in drought years, are associated with decreased abundance and diversity of breeding birds, which may be harbingers of compromised ecosystem integrity. Further experimentation with the timing, volume, and duration of spring snowmelt pulses is warranted. Managers should continue to monitor willow health and recruitment in Poopenaut Valley to meet the third goal.

Reducing variation in flow throughout the year in order to reduce the number of low flow days would likely be detrimental to the bird community. Regulated systems that “smooth out” the hydrograph (e.g., decrease peak flows and increase base flows) exert myriad detrimental impacts on downstream ecology, including creating conditions more conducive to colonization by invasive species (Bunn & Arthington, 2002), altering the normal composition of both zooplankton and aquatic plant communities in temporary wetlands like those found in Poopenaut Valley (Brock, Nielsen, Shiel, Green, & Langley, 2003), altering plant community composition from that adapted to the extremes to that adapted to more constant conditions (Vivian et al., 2014), and reducing temporal and spatial heterogeneity in habitat important to aquatic community diversity when droughts within historic normal are altered or eliminated (Boulton, Sheldon, Thoms, & Stanley, 2000). Mimicking the shape of the natural hydrograph of the Tuolumne River has been an overarching goal since this study's inception, and provides a good starting point for future managed hydrographs with tweaks due to studies like this and further experimentation with flows.

Dam managers have a unique opportunity to design water releases for the benefit of ecological communities downstream, which is becoming increasingly important in our changing climate (Acreman et al., 2014). In our study system, designing water releases that incorporate findings from this study, in conjunction with continued experimentation and monitoring, will yield the best adaptive management results for the birds and associated riparian habitat downstream of Hetch Hetchy Reservoir.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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APPENDIX

TABLE A1 Birds need food, shelter, and nesting sites in order to survive and reproduce

Variable	Influence on resources birds need	Citations
Average daily flow	1. Overland flow of water out of the stream channel and across wetlands is positively associated with the abundance of aquatic invertebrate taxa which are especially sensitive to habitat quality in montane wet meadows 2. Sierra Nevada wet meadows and seasonal ponds supported by overbank flows support a complementary invertebrate community to that found in the stream channel 3. Appropriate groundwater levels are the primary determinant of vegetation community composition; wet meadows depend on a shallow water table for persistence 4. Water under nests in wetlands reduces predator access and increases nesting success 5. Increased investment in leaf growth when enough water is available contributes to nest concealment, and nest concealment is positively correlated with nesting success and fledgling survival 6. Higher plant moisture levels contribute positively to terrestrial invertebrate community composition and biomass by providing a refuge from desiccation, a humid microclimate, and a source of water for ingestion	1. Holmquist, Jones, Schmidt-Gengenbach, Pierotti, and Love (2011) 2. Holmquist & Schmidt-Gengenbach (2012); Holmquist and Schmidt-Gengenbach (2020) 3. Lowry, Loheide II, Moore, and Lundquist (2011) 4. Picman et al. (1993); Cain et al. (2003); Hoover (2006); Lima (2009) 5. Eziz et al. (2017); Lima (2009); Caldwell et al. (2013) 6. Wenninger and Inouye (2008)
Days below the 25th percentile	1. Decreased discharge and flow velocity is associated with decreased habitat quantity and quality for aquatic invertebrates, leading to a reduction in invertebrate species diversity and lower percent Ephemeroptera, Plecoptera, and Tricoptera taxa 2. Low flows encourage invertebrates to behaviorally enter the drift and this has the potential to impact later emergence volumes 3. Wetlands flooded infrequently, or for short durations exhibit reduced invertebrate abundance, biomass, and productivity 4. Sufficient discharge during the low-flow season is important for riparian vegetation recruitment, especially cottonwood and willow species 5. Decreased water availability is associated with reductions in plant recruitment, annual growth, survival, primary productivity, biomass, nutritional content for herbivores, and reproductive output 6. The elimination of overbank flooding due to low flows reduces the growth rates of riparian species	1. Dewson, James, and Death (2007); Holmquist and Waddle (2013) 2. Brittain and Eikeland (1988) 3. Gladden and Smock (1990); Batzer and Wissinger (1996) 4. Rood et al. (2003) 5. Herrera (1998); Eziz et al. (2017); Rai, Klein, and Walter (2018); Saracco et al. (2018) 6. Reily and Johnson (1982)
Julian date of maximum release	1. Mismatches between peak runoff and nest initiation, more common in regulated systems, can cause nest failure by flooding; some species will then abandon the area	1. Brown and Johnson (1985); Graf, Stromberg, and Valentine (2002)
Instantaneous maximum release volume	1. Periodic high flow events scour the streambed. On short time scales this can result in reductions to invertebrate populations, but in the long term can lead to increased invertebrate diversity.	1. Brittain and Eikeland (1988)
Years since median	1. Inter-annual dry periods contribute to conifer invasion of Sierra Nevada wet meadows, altering light and soil moisture for herbaceous plants 2. In general, chronic low-flows (often associated with dams) contribute to altered plant communities favoring more homogeneous late-successional vegetation 3. Supra-seasonal drought can reduce aquatic invertebrate species richness and extirpate benthic invertebrate communities depending on the availability of refugia 4. Severe drought can impact the age structure of invertebrate communities for long periods following drying events (10+ years) if colonization is slow due to loss of habitat connectivity	1. Ratliff (1985); Lubetkin, Westerling, and Kueppers (2017) 2. Harris, Fox, and Risser (1987); Stromberg (2001) 3. Ledger, Brown, Edwards, Milner, and Woodward (2013); Boulton (2003); Lake (2003) 4. Resh (1992)

Note: Here, we provide examples of how aspects of the flow regime included in the model selection process can influence resources needed by birds during the breeding season.

TABLE A2 Avian species detected by area search in Poopenaut Valley and point count in Yosemite Valley during the course of this study

Common name	Scientific name	Poopenaut Valley	Yosemite Valley
Acorn woodpecker	*Melanerpes formicivorus*	x	x
American dipper	*Cinclus mexicanus*	x	x
American robin	*Turdus migratorius*	x	x
Anna's hummingbird	*Calypte anna*	x	x
Belted kingfisher	*Megaceryle alcyon*	x	x
Blue-gray gnatcatcher	*Megaceryle alcyon*	x	x
Brown-headed cowbird	*Molothrus ater*	x	x
Black-headed grosbeak	*Pheucticus melanocephalus*	x	x
Blue grosbeak	*Passerina caerulea*		x
Black phoebe	*Sayornis nigricans*	x	x
Black swift	*Cypseloides niger*		x
Brewer's blackbird	*Euphagus cyanocephalus*	x	x
Brown creeper	*Certhia americana*	x	x
Band-tailed pigeon	*Patagioenas fasciata*	x	x
Black-throated gray warbler	*Setophaga nigrescens*	x	x
Bullock's oriole	*Icterus bullockii*	x	x
Bushtit	*Psaltriparus minimus*	x	x
Cassin's finch	*Haemorhous cassinii*		x
California towhee	*Melozone crissalis*		x
Calliope hummingbird	*Selasphorus calliope*	x	
Canada goose	*Branta canadensis*	x	x
Canyon wren	*Catherpes mexicanus*	x	
California scrub-jay	*Aphelocoma californica*	x	
Cassin's vireo	*Vireo cassinii*	x	x
Chestnut-backed chickadee	*Poecile rufescens*		x
Cedar waxwing	*Bombycilla cedrorum*		x
Chipping sparrow	*Spizella passerine*	x	x
Common merganser	*Mergus merganser*	x	x
Common raven	*Corvus corax*		x
Dark-eyed junco	*Junco hyemalis*	x	x
Downy woodpecker	*Picoides pubescens*	x	x
Dusky flycatcher	*Empidonax oberholseri*	x	
European starling	*Sturnus vulgaris*		x
Evening grosbeak	*Coccothraustes vespertinus*	x	
Golden-crowned kinglet	*Regulus satrapa*		x
Gray flycatcher	*Empidonax wrightii*	x	
Hammond's flycatcher	*Empidonax hammondii*		x
Hairy woodpecker	*Picoides villosus*	x	x
Hermit warbler	*Setophaga occidentalis*		x
House wren	*Troglodytes aedon*	x	x
Hutton's vireo	*Vireo huttoni*	x	
Lawrence's goldfinch	*Spinus lawrencei*	x	
Lazuli bunting	*Passerina amoena*	x	x
Lesser goldfinch	*Spinus psaltria*	x	x
Lincoln's sparrow	*Melospiza lincolnii*	x	x
Mallard	*Anas platyrhynchos*	x	x
MacGillivray's warbler	*Geothlypis tolmiei*	x	x

TABLE A2 (Continued)

Common name	Scientific name	Poopenaut Valley	Yosemite Valley
Mountain chickadee	*Poecile gambeli*		x
Mourning dove	*Zenaida macroura*	x	
Mountain quail	*Oreortyx pictus*	x	
Nashville warbler	*Oreothlypis ruficapilla*	x	x
Northern flicker	*Colaptes auratus*	x	x
Northern rough-winged swallow	*Stelgidopteryx serripennis*	x	x
Nuttall's woodpecker	*Picoides nuttallii*	x	x
Olive-sided flycatcher	*Contopus cooperi*	x	
Orange-crowned warbler	*Leiothlypis celata*		x
Pine siskin	*Spinus pinus*	x	
Pileated woodpecker	*Dryocopus pileatus*		x
Pacific slope flycatcher	*Empidonax difficilis*	x	x
Purple finch	*Haemorhous purpureus*	x	
Red-breasted nuthatch	*Sitta canadensis*	x	x
Red-breasted sapsucker	*Sphyrapicus ruber*		x
Red-winged blackbird	*Agelaius phoeniceus*	x	x
Song sparrow	*Melospiza melodia*	x	x
Spotted sandpiper	*Actitis macularius*	x	x
Spotted towhee	*Pipilo maculatus*	x	x
Steller's jay	*Cyanocitta stelleri*	x	x
Swainson's thrush	*Catharus ustulatus*		x
Tree swallow	*Tachycineta bicolor*		x
Violet-green swallow	*Tachycineta thalassina*	x	x
Warbling vireo	*Vireo gilvus*	x	x
Western kingbird	*Tyrannus verticalis*	x	x
Western meadowlark	*Sturnella neglecta*	x	x
Western tanager	*Piranga ludoviciana*	x	x
Western wood-pewee	*Contopus sordidulus*	x	x
White-headed woodpecker	*Picoides albolarvatus*	x	x
Wilson's warbler	*Cardellina pusilla*	x	x
White-throated swift	*Aeronautes saxatalis*		x
Yellow-breasted chat	*Icteria virens*	x	
Yellow warbler	*Setophaga petechia*	x	x
Yellow-rumped warbler	*Setophaga coronata*	x	x

Note: The species in this table are those included in statistical analyses.