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RESEARCH ARTICLE

Species-specific responses to wetland mitigation among amphibians in the Greater Yellowstone Ecosystem

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Habitat loss and degradation are leading causes of biodiversity declines, therefore assessing the capacity of created mitigation wetlands to replace habitat for wildlife has become a management priority. We used single season occupancy models to compare the occurrence of larvae of four species of pond-breeding amphibians in wetlands created for mitigation, wetlands impacted by road construction, and unimpacted reference wetlands along a highway corridor in the Greater Yellowstone Ecosystem, United States. Created wetlands were shallow and had less aquatic vegetation and surface area than impacted and reference wetlands. Occupancy of barred tiger salamander (*Ambystoma mavortium*) and boreal chorus frog (*Pseudacris maculata*) larvae was similar across wetland types, whereas boreal toads (*Anaxyrus boreas*) occurred more often in created wetlands than reference and impacted wetlands. However, the majority of created wetlands (>80%) dried partially or completely before amphibian metamorphosis occurred in both years of our study, resulting in heavy mortality of larvae and, we suspect, little to no recruitment. Columbia spotted frogs (*Rana luteiventris*), which require emergent vegetation that is not common in newly created wetlands, occurred commonly in impacted and reference wetlands but were found in only one created wetland. Our results show that shallow created wetlands with little aquatic vegetation may be attractive breeding areas for some amphibians, but may result in high mortality and little recruitment if they fail to hold water for the entire larval period.

Key words: **amphibians, Clean Water Act, created wetlands, Greater Yellowstone Ecosystem, occupancy models, wetland mitigation, wetland restoration**

Implications for Practice

- Our work in the Greater Yellowstone Ecosystem shows that it is possible to create mitigation wetlands that are used as breeding sites by native amphibians.
- However, the minimum hydroperiod requirements of all target species should be considered when designing mitigation wetlands. If created wetlands dry prior to metamorphosis of amphibian larvae, heavy mortality can occur.
- Building wetlands resistant to early drying is particularly important because of the expected effects of a changing climate on wetlands in the Intermountain West.

Introduction

Widespread wetland loss from agriculture, development, and climate change has contributed to population declines across taxa (Gibbs 2000; Gallant et al. 2007; Quesnelle et al. 2013). In recent decades, growing awareness of these declines resulted in legislation protecting wetlands, including Section 404 of the Clean Water Act. Under Section 404, discharge of dredged or fill materials into waters of the United States, including many wetlands, is prohibited without a permit from the U.S. Army Corps of Engineers. Today, the Corps' permitting process is largely guided by the 1989 executive policy of "no net loss" of wetlands: any loss of wetland area must be mitigated by an equal or greater area gained, achieved through either wetland restoration or construction (U.S. EPA 1990; Hough & Robertson 2008). While this policy and others have been successful at slowing the loss of wetland area, the capacity of created wetlands to replace natural wetland functions, including supporting a full host of native organisms, remains uncertain (Dahl 2011; Moreno-Mateos et al. 2012).

Many North American amphibians rely on wetlands for survival and reproduction. Furthermore, because many amphibian species worldwide have experienced dramatic declines caused by habitat alteration and destruction, the question of whether created and restored wetlands support viable amphibian populations is important for conservation (Stuart et al. 2004; Collins et al. 2009). Created wetlands can be beneficial for many species, but these benefits are often species-specific and dependent upon wetland design features (Brown et al. 2012). For example, high vegetation cover, lack of predatory fish, and

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presence of shallow-sloped littoral zones increased amphibian diversity in created wetlands in Missouri, but even in wetlands with desired features, some species were rarely encountered (Shulse & Semlitsch 2012). Better understanding of the design features of created wetlands supporting specific amphibian species will result in better mitigation practices and wildlife policies.

Amphibians use wetlands of a variety of hydroperiods from temporary to permanent, and managers who design mitigation wetlands face the challenge of replicating this natural hydrologic variation (Wellborn et al. 1996). An ongoing problem has been the replacement of temporary wetlands with less complex, permanent, open-water ponds that do not function the same as the original wetlands (Dahl 2011). Permanent ponds are vulnerable to invasion by predatory fish and other species, such as American bullfrogs (*Lithobates catesbeianus*), which can reduce survival of native amphibians and alter community structure outside their native range (Pearl et al. 2005; Shulse et al. 2013; Hossack et al. 2017). Consequently, it is becoming common for mitigation plans to require construction of more complex temporary wetlands, which poses new issues for wetland design (Lichko & Calhoun 2003; Calhoun et al. 2014). For instance, predicting the depth required to produce a specific hydroperiod is difficult because of variable soil characteristics and inter-annual variation in precipitation and water table height (Shulse et al. 2010). If the wetland is too deep, the hydroperiod of the wetland will be permanent, risking colonization by invasive species and fish. If the wetland is too shallow, the hydroperiod of the wetland may be too temporary, and the wetland may dry before amphibian larvae metamorphose. In both scenarios, mitigation wetlands have the potential to act as population sinks or ecological traps, luring amphibians to immigrate and breed, but resulting in high larval mortality and little to no recruitment (Dimauro & Hunter 2002; Schlaepfer et al. 2002).

The effects of global climate change also complicate the design of mitigation wetlands. Small isolated wetlands often rely on precipitation to fill, which makes them particularly vulnerable to drying quickly during drought conditions (Brooks 2009; Matthews 2010). In the Greater Yellowstone Ecosystem (GYE), where we conducted our study, hotter and drier summers, increased evapotranspiration, earlier run-off, and decreased snowpack have been associated with earlier drying of natural wetlands (Sepulveda et al. 2015; Ray et al. 2016). These changes are likely contributing to population declines of amphibians that occur in the region (Hossack et al. 2015; Ray et al. 2016), and further underscore the importance of evaluating the capacity of created mitigation wetlands to support native amphibians.

Here, our goal was to take advantage of recent mitigation efforts along a highway corridor in northwest Wyoming to evaluate differences in occurrence of native amphibians among created, impacted, and reference wetlands and identify environmental and design features associated with species occupancy. Most of the created wetlands were not designed to benefit wildlife explicitly, but amphibians are often attracted to and breed in created habitats, making it important to evaluate the potential effects of wetland creation on local amphibian populations (Pearl & Bowerman 2006). We included impacted wetlands in this study because development does not always cause complete destruction of a wetland, but often damages or impairs just a portion of the wetland. Four amphibian species occur in this area: barred tiger salamanders (*Ambystoma mavortium*), boreal toads (*Anaxyrus boreas*), Columbia spotted frogs (*Rana luteiventris*), and boreal chorus frogs (*Pseudacris maculata*). A fifth species, the northern leopard frog (*Lithobates pipiens*), occurred in the area historically but has been extirpated (Ray et al. 2014).

All four extant species require standing water for breeding, oviposition, and larval development, and spend much of their adult lives in the terrestrial environment surrounding breeding ponds, but they differ in several key life history traits that may influence their use of created wetlands. Compared with the three anuran species that must complete metamorphosis in a single season, tiger salamanders can overwinter as larvae (Werner et al. 2004). Because the majority of created wetlands in our study area were designed to have temporary-to-intermediate hydroperiods, we predicted that tiger salamanders would occur in few created wetlands and instead select reference and impacted breeding sites that retain water throughout the year, providing ample time for larvae to metamorphose (Hossack et al. 2015). Similarly, Columbia spotted frogs are highly aquatic and generally breed in large water bodies with abundant vegetation (Hossack et al. 2015; Ray et al. 2016), so we expected this species to occur more frequently in reference and impacted wetlands than in created wetlands. In contrast to tiger salamanders and Columbia spotted frogs, boreal toads and boreal chorus frogs will breed in temporary wetlands (Ray et al. 2016). Boreal toads often colonize and breed in habitats immediately after disturbance such as wildfire and pond construction (Pearl & Bowerman 2006; Guscio et al. 2008; Hossack et al. 2013*b*). Therefore, we expected boreal toads and boreal chorus frogs to occur in a high proportion of created wetlands.

Methods

Study Area

To mitigate wetland loss and impacts associated with the reconstruction of Highway 287/26 over Togwotee Pass between Moran and Dubois, Wyoming, the Wyoming Department of Transportation (WYDOT) constructed new wetlands along the highway corridor between 2005 and 2014. Wetlands were located in the Bridger-Teton National Forest, approximately 12 km east of Grand Teton National Park (Fig. 1). Created wetlands were excavated with heavy equipment down to the water table and planted with a wetland seed mix and willow (*Salix* spp.) cuttings. Impacted wetlands were natural wetlands altered by road construction (e.g., modified banks, some filling, and erosion control) but not completely destroyed. Most wetland impacts were limited to a small portion of the wetland perimeter (i.e., <25%). Reference wetlands were natural wetlands that did not sustain impacts from road construction and thus provided a baseline against which to compare created and impacted sites. Wetland types did not significantly differ in measured

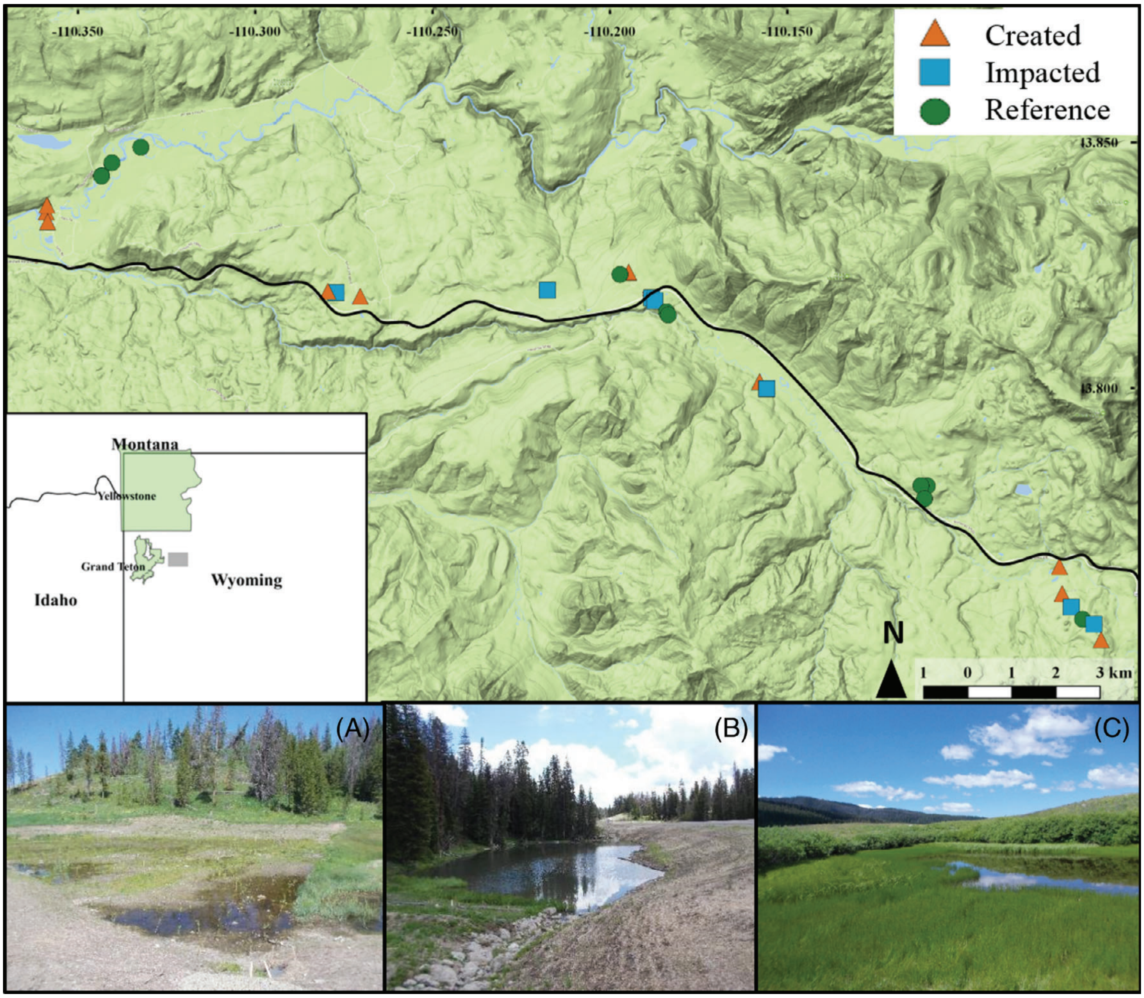

Figure 1. Locations of wetlands sampled for amphibians near Moran, Wyoming (gray inset) in 2015 and 2016 to determine differences in abundance and occurrence among created (A), impacted (B), and reference (C) wetlands. Representative photos illustrate each wetland type. The black line is U.S. Highway 26-287. Figure adapted from Swartz et al. (2019).

water chemistry variables (pH, conductivity; Swartz et al. 2017, 2019).

We selected study wetlands by identifying all created wetlands that held water in June 2014, then selected the impacted and reference wetlands nearest to each of these created wetlands (Table S1). Created wetlands were constructed on average 274.4 m (SD = 156.77 m) from the nearest natural wetland. Wetlands ranged in elevation from 2,100 to 3,050 m above sea level. Surrounding vegetation at high elevations was dominated by conifer forest that included species such as lodgepole pine (*Pinus contorta*), whitebark pine (*Pinus albicaulis*), Engelmann spruce (*Picea engelmannii*), and Douglas fir (*Pseudotsuga menziesii*). Lower elevations were dominated by grassland vegetation ground covers such as mixed sagebrush (*Artemisia* spp.). This area is characterized by long, cold winters with heavy snowfall and short, cool summers. Wetlands filled from snowmelt between early May (lower elevations) and early June (higher elevations). April 1st snow water equivalent measurements from the top of Togwotee Pass were 99.54 and 99.07% of the 30-year median in 2015 and 2016, respectively (https://wcc.sc.egov.usda.gov/nwcc/site?sitenum=822).

Sampling

In 2015 and 2016, we sampled all four species of amphibian larvae, counted Columbia spotted frog egg masses, and measured habitat characteristics in created, impacted, and reference wetlands (n = 10, 7, and 10, respectively). Two created wetlands were not deep enough to sample at any point in the summer of 2015, but were sampled in 2016 (Table S1).

Habitat Characteristics. We developed an a priori list of environmental and design characteristics that could influence occurrence of amphibians across all wetland types. To estimate wetland area, we used the area estimation tool in a Garmin e-trex Global Position System. We defined wetland area as the portion of the wetland that held water in early June of 2015, when wetlands achieved their maximum size.

We measured maximum depth at the same time as wetland area in June. We extracted elevation and identified the nearest natural (reference or impacted) wetland using Google Earth (version 7.1.7.2606). We estimated aquatic vegetation cover in late July, using a 1-m^2 quadrat every 80 m along the wetland shore, both at 1 m and 5 m from the water's edge. We also recorded presence of fish when we detected them visually or in traps (see below).

Amphibian Sampling. We sampled amphibian larvae using a combination of collapsible mesh and plastic minnow traps placed at 20-m intervals around the perimeter of each wetland (range = 1–48 traps/wetland; Griffiths 1985; Adams et al. 1997). Traps were placed at depths of approximately 20–30 cm. We left traps open for two consecutive 24-hour periods every 2 weeks during larval development (mid-June to late-July) and counted the number of each species of larval amphibian in each trap during each period. Dates of surveys differed among sites due to differences in timing of breeding and larval development across elevations. However, at all sites we began sampling as soon as free-swimming larvae were large enough to be trapped, and we stopped when we found metamorphosed individuals or when wetlands dried.

To increase detection probability of species that may be less likely to enter traps, we also conducted a dip-net sweep 1 m from each trap before checking that trap. Due to time limitations in 2015, we stopped trapping at a site if no amphibians of any species were encountered during the first two sampling occasions. However, these wetlands were all revisited several times throughout the season and surveyed visually to ensure that they were unoccupied. In 2016, we increased sampling effort to ensure a minimum of four sampling occasions at each wetland, with the exception of one site that dried after the two sampling occasions.

Egg Mass Surveys. To provide an additional measure of Columbia spotted frog occurrence and abundance, we counted egg masses by walking the entire shoreline and other shallow areas of each wetland. Columbia spotted frogs lay conspicuous egg masses that can be used as a reliable index of the number of breeding females (Licht 1975). The egg masses float near the water's surface and are typically laid communally near the shore, making them easy to detect. To reduce counting errors, each egg mass was marked with a colored toothpick (Hossack et al. 2013*c*). We began surveying wetlands as soon as ice melted (late April/early May) and visited each wetland at least once per week until the count of egg masses did not change for two consecutive visits and there was no change in counts in neighboring wetlands (Hossack et al. 2013*c*).

Statistical Methods

To estimate occupancy, we analyzed larval amphibian occurrence data using single season occupancy models implemented in the R package unmarked (MacKenzie et al. 2002; Fiske & Chandler 2011). Occupancy models use species detection/nondetection data from repeated site visits to estimate ψ, the probability that a site is occupied, and p_j, the probability of detecting the species, given presence, in survey *j*. An important assumption of these models is that occupancy state within a site is closed for the duration of the sampling season. Because all amphibian species in our study area breed around the same time (late-April to late-May, depending on elevation; Werner et al. 2004) and larvae are restricted to a particular wetland until metamorphosis, we satisfied this assumption by beginning trapping when larvae were free-swimming and large enough to be trapped and ceasing trapping when we detected metamorphs of all anuran species, or when a wetland dried. Because tiger salamanders take much longer to metamorphose than the other species in our study area, we never detected tiger salamander metamorphs at any site (Werner et al. 2004).

We used a multi-stage model selection process to identify the best model structure for detection and occupancy separately. In addition to testing for differences in occupancy among the three wetland types, we were interested in whether other environmental and design features helped to explain differences in detection and occurrence for each species. Therefore, we also included covariates describing wetland size, maximum depth, percent cover of aquatic vegetation, and elevation. First, we set occupancy to be constant and fit detection-only models with linear effects of sampling period, wetland area, percent cover of aquatic vegetation, depth, and year (2015 or 2016). We used backwards stepwise selection to eliminate the covariate with the least partial significance. At each step we monitored Akaike information criterion (AIC) and if removing a variable increased AIC we retained it even if that variable was not significant. Using the top model for detection, we started with a global occupancy model that included wetland type (created, impacted, reference), year, percent cover of aquatic vegetation, maximum depth, wetland area, and elevation. As with the detection portion of the model, we used backwards stepwise selection to identify the most parsimonious model for occupancy. We retained wetland type in the model even if it was not significant because it was the variable of primary interest.

We scaled all continuous explanatory variables by subtracting the mean and dividing by the standard deviation. We excluded collinear explanatory variables from the same models (Pearson's $r > 0.7$; Dormann et al. 2013) and assumed that the effects of wetland type and other covariates were consistent between years. We assessed goodness of fit (GOF) for the top detection model and global occupancy model for each species with a Pearson chi-square test implemented using mb.gof.test function in the AICcmodavg package (Mazerolle 2019). We used 5,000 bootstrapped iterations to test GOF and estimate overdispersion (MacKenzie & Bailey 2004).

Because the Columbia spotted frog egg mass count data contained many zeros, we were unable to fit a mixed-effects model to account for 2 years of sampling at each site. Instead, we analyzed differences in egg mass counts among created, impacted, and reference wetlands using a negative binomial generalized linear model with the mean count for each site (rounded to the nearest integer) as the response variable.

Table 1. Mean (SD) of measured physical habitat characteristics of created, impacted, and reference wetlands in Northwest Wyoming that were surveyed for amphibians in 2015 and 2016.

	Created		*Impacted*		*Reference*	
Variable	*2015 (n = 8)*	*2016 (n = 10)*	*2015 (n = 7)*	*2016 (n = 7)*	*2015 (n = 10)*	*2016 (n = 10)*
Max depth (cm)	38.4 (25.6)	44.4 (34.2)	124.1 (45.6)	113.3 (32.9)	111.7 (35.8)	100.2 (31.3)
Aquatic vegetation (% cover)	24.1 (29.5)	27.3 (33.0)	46.4 (33.4)	70.4 (50.3)	49.4 (33.1)	60.7 (39.6)
	Both years		Both years		Both years	
Wetland area (m^2)	2,644.7 (3,768.8)		5,377.7 (3,637.7)		3,678.0 (3,773.2)	
Elevation (m)	2,515.5 (342.2)		2,678.1 (182.5)		2,556.8 (329.6)	

Results

In 2015, we trapped 109 tiger salamander larvae, 1,290 boreal toad tadpoles, 372 boreal chorus frog tadpoles, and 239 Columbia spotted frog tadpoles over 108 trapping occasions at 25 wetlands. In 2016, we trapped 68 tiger salamander larvae, 391 boreal toad tadpoles, 425 boreal chorus frog tadpoles, and 252 Columbia spotted frog tadpoles over 134 trapping occasions at 27 wetlands. Naïve species richness (unadjusted for detection probability) over the whole study was highest in reference wetlands (mean = 2.00 species, range = 0–4 species), followed by impacted wetlands (mean = 1.57, range = 0–3 species) and created wetlands (mean = 1.30 species, range = 0–4 species).

Created wetlands were smaller, had less aquatic vegetation, and were shallower than reference and impacted wetlands (Table 1). Created wetlands also had shorter hydroperiods than reference and impacted wetlands. In both years, a majority of created wetlands dried partially (i.e. at least one isolated pool dried completely) or completely by the end of July (2015 = 90%, 2016 = 80%; Table S1). No reference or impacted wetlands dried over the same time period. Habitat characteristics in reference and impacted wetlands were similar (Table 1). We detected fish in two impacted and one reference wetland, all of which were permanent and had a stream or river connection.

Tiger Salamanders

We detected tiger salamander larvae in 13 of 27 wetlands (3 of 10 created, 3 of 7 impacted, and 7 of 10 reference). The model for detection probability showed that detection decreased with increasing aquatic vegetation ($\beta_{veg} = -1.36$, SE = 0.28). Including wetland area marginally improved model fit (ΔAIC = 1.09), so we retained it even though it was not statistically significant ($\beta_{wetland\_area} = 0.33$, SE = 0.20). Mean detection probability (when covariates were set to their mean value) was 0.68 (SE = 0.06). Occupancy probability did not differ by wetland type (Fig. 2) but decreased with increasing elevation ($\beta_{elevation} = -1.36$, SE = 0.45). We found no evidence of lack of fit or overdispersion (c-hat = 0.69, $p = 0.45$).

Boreal Toads

We detected boreal toads in 6 of 27 wetlands (4 of 10 created, 0 of 7 impacted, and 2 of 10 reference). Because of the low and uneven occurrence of boreal toads across wetland types (i.e. no detections in impacted wetlands), models that included wetland type did not converge. Detection increased with wetland area ($\beta_{wetland\_area} = 2.85$, SE = 1.18) and decreased with depth ($\beta_{depth} = -3.17$, SE = 1.40) and aquatic vegetation ($\beta_{veg} = -4.47$, SE = 1.45). Mean detection probability was 0.70 (SE = 0.18). Elevation was the only covariate supported in our top occupancy model, which indicated occupancy decreased with increasing elevation ($\beta_{elevation} = -1.79$, SE = 0.55). Given our high probability of detection and high number of site visits (i.e. with a mean detection probability of 0.70 on each visit we would have $p = 1 - [1-0.70]^6 = 0.999$ of detecting boreal toads at least once), we are confident that our raw data provide an accurate representation of toad occupancy across our study wetlands (Fig. 2). We found no evidence of lack of fit or overdispersion (c-hat = 0.64, $p = 0.42$).

Boreal Chorus Frogs

We detected boreal chorus frogs in 17 of 27 wetlands (6 of 10 created, 5 of 7 impacted, and 6 of 10 reference wetlands). The best detection probability model showed that detection probability was higher in 2016 than 2015 ($\beta_{year} = 0.87$, SE = 0.39), increased with wetland size ($\beta_{wetland\_area} = 0.44$, SE = 0.23), and decreased through the summer ($\beta_{prim} = -0.89$, SE = 0.23) and with maximum depth ($\beta_{depth} = -0.72$, SE = 0.33). Mean detection probability was 0.94 (SE = 0.04). Occupancy probability did not differ by wetland type (Fig. 2) but increased with increasing aquatic vegetation ($\beta_{veg} = 1.27$, SE = 0.75) and decreased with increasing elevation ($\beta_{elevation} = -2.06$, SE = 0.91). Including wetland area in our occupancy model marginally improved model fit (ΔAIC = 0.95), so we retained it even though it was not statistically significant ($\beta_{wetland\_area} = -1.26$, SE = 0.20). We found no evidence of lack of fit or overdispersion (c-hat = 1.07, $p = 0.32$).

Columbia Spotted Frogs

We detected Columbia spotted frog larvae in 9 of 27 wetlands (1 of 10 created, 3 of 10 impacted, and 5 of 10 reference wetlands). Our top model for detection probability included just a positive effect of wetland size on detection probability ($\beta_{wetland\_area} = 0.91$, SE = 0.36). Mean detection probability was 0.82 (SE = 0.05). Columbia spotted frogs occurred in a higher proportion of reference and impacted wetlands

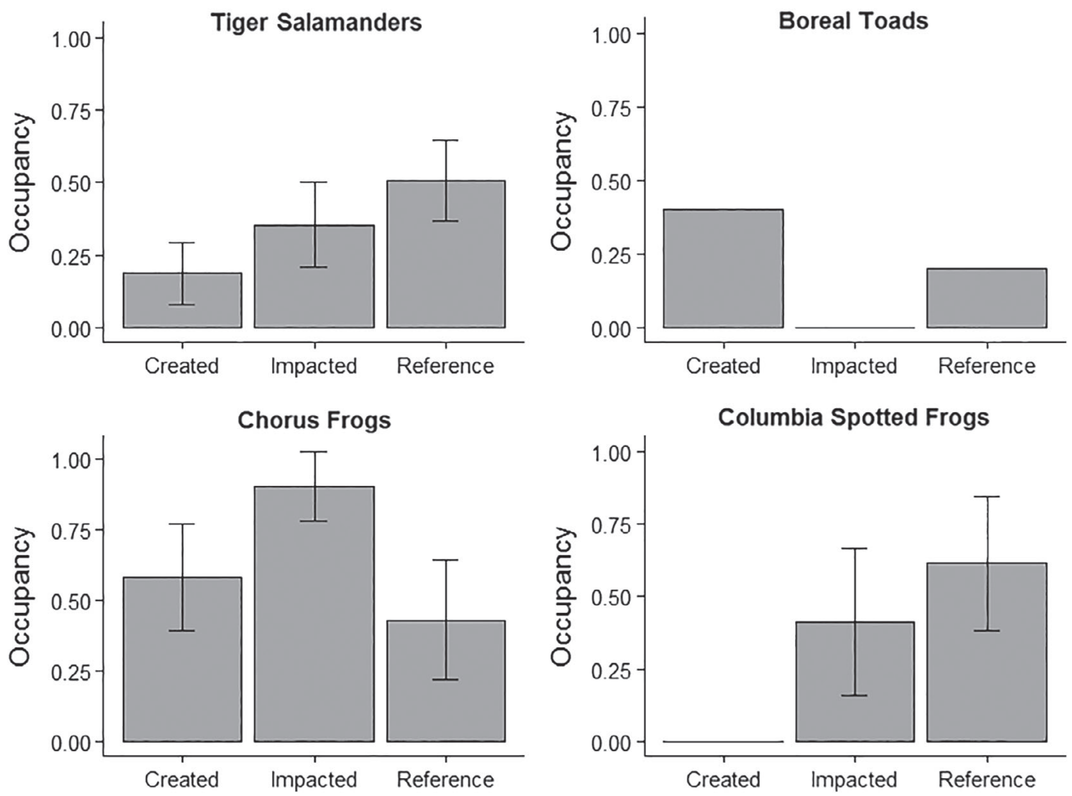

Figure 2. Estimated proportion of sites occupied by larval amphibians by wetland type from single season occupancy when all other covariates were set to their mean values. Models for boreal toads that included wetland type did not converge, so the plot shows raw occupancy data. Error bars represent ±1 SE.

than created wetlands (Fig. 2). Occupancy increased with aquatic vegetation (β_{veg} = 1.08, SE = 0.58) and wetland area ($\beta_{wetland\_area}$ = 2.25, SE = 1.00). Including maximum depth and year marginally improved model fit, so we retained them even though they were not statistically significant (β_{depth} = −1.25, SE = 0.92; β_{year} = −1.43, SE = 1.05). We found no evidence of lack of fit or overdispersion (c-hat = 1.01, p = 0.20).

We found Columbia spotted frog egg masses in the same nine wetlands where we detected larvae. Egg mass counts ranged from 0 to 49 per site. Abundance of egg masses in reference (estimated mean = 7.45 egg masses, SE = 5.56) and impacted wetlands (mean = 7.43, SE = 6.95) was much higher than in created wetlands (estimated mean = 0.20, SE = 0.21).

Discussion

Our results show variable species-specific responses to wetland mitigation at our study sites, and highlight both the opportunities and challenges associated with constructing wetlands that support a full assemblage of native amphibians. Consistent with studies from other regions, amphibians quickly colonized newly created wetlands (Lehtinen & Galatowitsch 2001; Balcombe et al. 2005; Shulse et al. 2010). Tiger salamanders and chorus frogs occurred at similar rates in created and reference wetlands, whereas boreal toads occurred more frequently in created wetlands and spotted frogs occurred more frequently in reference and impacted wetlands. We found that created wetlands were shallower, smaller, and had less aquatic vegetation than reference wetlands, while impacted wetlands did not differ from reference wetlands in measured environmental variables. However, most of these created wetlands partially or completely dried by the end of July in both study years, likely resulting in partial or complete mortality of amphibian larvae before metamorphosis occurred.

Contrary to our prediction, tiger salamanders occurred across all wetland types, including in three created wetlands. Tiger salamander larvae require water bodies with a long hydroperiod to survive over winter (Werner et al. 2004). While depth did not emerge as an important predictor of salamander occurrence, the three created wetlands where tiger salamanders were detected were deeper, on average, than the other created wetlands (mean depth where detected = 58.4 cm vs. mean in others = 33.5 cm). Likewise, boreal chorus frog larvae were common and occurred evenly across all wetland types. The probability of chorus frog occupancy increased with percent cover of aquatic vegetation and decreased with wetland size, indicating a preference for small, highly vegetated wetlands. This pattern is consistent with previous work from the GYE showing an increase in chorus frog occupancy with vegetation cover (Gould et al. 2012). Of our four study species, chorus frogs metamorphose the earliest and often use small ephemeral wetlands to breed (Ray et al. 2016).

Consistent with long-term monitoring in Yellowstone and Grand Teton national parks, as well as across their range in the western United States, we detected boreal toads in relatively few wetlands (Corn et al. 2005; Wente et al. 2005; Hossack et al. 2015). Even so, toads occupied nearly half of the created wetlands in our study. Boreal toads are of particular conservation concern in this region as they have experienced dramatic population declines over large portions of their range, including within protected areas such as the GYE, and now occupy <2% of available breeding sites in Yellowstone and Grand Teton national parks (Muths et al. 2003; Ray et al. 2016; Hossack 2017). Boreal toads are a Native Species of Greatest Conservation Need in Wyoming, and the U.S. Forest Service Region 2 considers them a sensitive species, making their use of created wetlands of particular interest to land managers. Boreal toads and chorus frogs are often early colonizers to wetlands after human and natural disturbances, including wetland creation and fire, where they select warm, shallow areas for breeding (Pearl & Bowerman 2006; Shulse & Semlitsch 2012; Hossack et al. 2013*b*). Population increases of toads following disturbance may be brief (e.g. fire; Hossack et al. 2013*b*) or long term (e.g. in beaver-created wetlands; Hossack et al. 2015). In Oregon, boreal toads colonized and bred in six newly created wetlands within the first years after construction, but breeding continued in only two of the six wetlands in subsequent years (Pearl & Bowerman 2006). Created wetlands may be susceptible to local extinctions due to drought, disease, or invasion of predators, especially if they are not designed to provide a complex array of habitat conditions to buffer year-to-year variation (Petranka et al. 2007). We did not observe changes in the wetlands occupied by boreal toads between the 2 years of our study, and longer-term data are needed to determine whether toads and other amphibian species are able to persist at created wetlands.

In contrast to the other three amphibian species, Columbia spotted frog larvae and egg masses were only detected in one created wetland, but were common in reference and impacted wetlands. Spotted frogs are the only extant amphibian in the study area that hibernates aquatically and this species commonly breeds in large wetlands with emergent vegetation (Pearl et al. 2007; Hossack et al. 2013*a*, 2015). The single created wetland where we detected spotted frog reproduction (Quarry) was constructed in 2008, and it is the second oldest created wetland in the study. We detected all four species of amphibians in Quarry, indicating that the design features present here—including intermediate hydroperiod, shallow littoral zones, and abundant aquatic vegetation—may be appropriate objectives for wetland mitigation in this region. Notably, Quarry also had the highest taxonomic richness of invertebrates of all the wetlands in this study (Swartz et al. 2019), suggesting that mitigation wetlands designed to provide complex habitat can benefit a wide range of species. Quarry was designed to have both shallow and deep habitats, and aquatic vegetation had developed to provide crucial habitat for spotted frog breeding (Pearl et al. 2007). Quarry is also deeper than most of the other created wetlands and holds water throughout the summer months in most years. With a sample size of one, we cannot be certain that the habitat complexity of Quarry resulted in the highest species richness of amphibians and invertebrates. However, further investigation of the characteristics of this site appears warranted.

In both years of this study, over 80% of created wetlands dried partially or completely prior to amphibian metamorphosis, which raises the concern that created wetlands could be population sinks or ecological traps for these species (i.e. low-quality habitats that are preferred over higher quality habitats; Battin 2004; Robertson et al. 2013; Hale & Swearer 2017). Even when created wetlands did not dry completely because of varied bottom topography, they were often reduced to multiple small, isolated pools that resulted in mortality of most larvae. Future studies could assess the possibility that created wetlands that dry early act as population sinks or ecological traps by using recruitment (i.e. survival to metamorphosis)—rather than presence of breeding adults, eggs, or tadpoles—as the metric of successful restoration (Grant et al. 2018). Information about amphibian species-specific larval survival and recruitment rates are crucial—but often missing—elements of demographic models used for amphibian conservation and monitoring (Biek et al. 2002; Che-Castaldo et al. 2018).

Overall, our results suggest that shallow created wetlands with little aquatic vegetation may be attractive breeding sites for the majority of native amphibians in the GYE, but further study is needed to determine how early wetland drying affects population growth, and whether these wetlands act as population sinks or ecological traps. Temporary and intermediate hydroperiod wetlands are important for amphibians and other wetland species because they are less likely to be invaded by vertebrate predators (Vasconcelos & Calhoun 2006; Shulse et al. 2013; Drayer & Richter 2016). However, wetlands with intermediate hydroperiods are difficult to create when precipitation and temperature are spatially and temporally variable, and creation can be problematic even when these conditions are stable (Kolozsvary & Holgerson 2016). The single wetland in our study area that supported breeding by all four native amphibians (Quarry) incorporated a variety of depths, including warm, shallow littoral zones and deeper areas where larvae could retreat as the wetland dried throughout the summer. These design elements may be good targets for wetland restoration in this region, and are likely to make wetlands resistant to early drying, which is particularly important in light of the forecasted changes in climate (Brooks 2009; Sepulveda et al. 2015) in the Intermountain Region and the likely effects of these changes on temporary and intermediate wetlands.

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Supporting Information

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

Table S1. Descriptions of wetlands surveyed for amphibians in 2015 and 2016.

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