Herpetological Conservation and Biology 21(1):85–100.
Received: 27 December 2023; Accepted: 5 November 2025; Published: 30 April 2026.

AMPHIBIAN USE OF RECENTLY CREATED WETLANDS IN THE PALOUSE REGION OF NORTHERN IDAHO, USA

ROLLIE M. GRINDER[1,5], CHARLES R. PETERSON[2], EDWARD O. GARTON[3], AND JAVAN M. BAUDER[4]

[1]Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona, USA
[2]Department of Biological Sciences, Idaho State University, Pocatello, Idaho, USA
[3]Department of Fish and Wildlife Resources, University of Idaho, Moscow, Idaho, USA
[4]U.S. Geological Survey, Arizona Cooperative Fish and Wildlife Research Unit,
University of Arizona, Tucson, Arizona, USA
[5]Corresponding author, e-mail: rolliegrinder@arizona.edu

Abstract.—**Human development has resulted in the loss of natural wetlands in many regions and thus has led to amphibian habitat loss. Human-constructed wetlands are increasingly prevalent, particularly in human-modified landscapes, and can be used as breeding habitats by amphibians. It is important to identify factors influencing amphibian use of constructed wetlands to guide future wetland creation efforts. We examined wetland- and landscape-level factors influencing the presence and reproduction of native amphibians in 33 recently created (2–11 y-old) wetlands within an urban-agricultural interface in northern Idaho, USA. We recorded wetland age, perimeter vegetation, and percentage of surrounding land cover as covariates and modeled detection and occupancy using Bayesian Multi-scale Occupancy Models for the three species we detected: Sierran Treefrog (*Pseudacris sierra*), Colombia Spotted Frog (*Rana luteiventris*), and Long-Toed Salamander (*Ambystoma macrodactylum*). Our results indicate that these three species can rapidly colonize recently created wetlands in an urban-agricultural interface. The effects of wetland- and landscape-scale features varied across species. Colombia Spotted Frog occupancy was greatest in older wetlands with some evidence for a negative association with more urbanized landscapes. Long-Toed Salamanders and Sierran Treefrogs were not associated with wetland age but also showed some evidence of negative associations with urbanization. Long-Toed Salamanders showed evidence of using less vegetated wetlands while Sierran Treefrogs showed evidence of using more vegetated wetlands. Our results are consistent with multiple studies showing that wetlands in human-modified landscapes can provide amphibian breeding habitat, and they suggest that including vegetation plantings within recently created wetlands may promote amphibian colonization. Anecdotal observations also indicate that designing wetlands with sufficient hydroperiod for metamorphoses may be important for ensuring that newly created wetlands benefit amphibian populations.**

Key Words.—*Ambystoma macrodactylum;* Long-Toed Salamander; *Pseudacris sierra*; *Rana luteiventris*; Sierran Treefrog; urbanization

INTRODUCTION

Habitat loss and fragmentation due to agricultural or urban development represent serious threats to many native amphibian species (Alford and Richards 1999; Stuart et al. 2004; Curado et al. 2011; Hamer et al. 2021). For example, agricultural or urban development may negatively affect pond-breeding amphibians through direct loss of aquatic breeding habitat and through loss or degradation of the upland habitats used by metamorphosed individuals (Semlitsch 2000, 2003; Cushman 2006). Additionally, agricultural and urban areas may act as barriers to amphibian dispersal and can isolate remaining populations (Lehtinen et al. 1999; Marsh and Trenham 2001; Parris 2006). Agricultural and urban development may also alter natural wetland hydroperiods (Richter and Azous 1995; Luo et al. 1997; Mayaja et al. 2017). This can facilitate the establishment of introduced predators such as fish (Hecnar and M'Closkey 1997; Porej and Hetherington 2005; Riley et al. 2005) and decrease water quality from chemical or sediment runoff (Bishop et al. 1999; Schade-Poole et al. 2016). These wetland and landscape alterations can negatively impact amphibian metapopulation dynamics and population persistence as well as overall wetland biodiversity.

Many amphibian species use anthropogenic wetlands, such as farm and irrigation ponds, as breeding habitat. These wetlands may provide important amphibian breeding habitat in landscapes where natural wetlands are scarce or absent (Laan and Verboom 1990; Beebee 1997; Baker and Halliday 1999; Knutson et al. 2004; Goldberg and Waits 2009). The creation of wetlands in human-modified landscapes can therefore be an important conservation tool for native pond-breeding amphibians, and native amphibians may rapidly (e.g., < 1 y) colonize newly created wetlands (Pechman et al. 2001; Petranka et al. 2007). Both landscape- and wetland-level characteristics may influence amphibian use of human-created wetlands. For example, amphibians may be less likely to use human-created wetlands in developed landscapes because of dispersal barriers such as open fields, roads, and other urban infrastructure (Kolozsvary and Swihart 1999; Lehtinen et al. 1999; Goldberg and Waits 2009). Urban development in the surrounding landscape may also lead to a lack of suitable upland habitat for foraging or over-wintering (Gibbons 2003; Porej et al. 2004). Wetland characteristics such as water quality (Griffis-Kyle et al. 2014; Kiesow and Griffis-Kyle 2017) and the availability of vegetation for egg laying sites (Porej and Hetherington 2005) can also affect amphibian use. Finally, amphibian species may respond differently to landscape- and wetland-level characteristics depending on their particular life histories and habitat requirements (Pearl et al. 2005; Goldberg and Waits 2009, 2010; Seaborn et al. 2021). Understanding species-specific factors influencing amphibian use of human-created wetlands is important to ensure that future wetland construction efforts provide the maximum possible benefit for pond-breeding amphibians.

The Palouse Region of northern Idaho, USA, has undergone dramatic landscape changes following Euro-American settlement in the late 1800s, which has resulted in dramatic declines in native wetlands (Black et al. 1998; Pocewicz et al. 2008). Now dominated by agriculture, human-created wetlands (e.g., ponds) are nevertheless widespread throughout this landscape, and many provide suitable breeding habitat for native pond-breeding amphibians (Monello and Wright 1999; Goldberg and Waits 2009). While these studies have examined the relationships between amphibian use of human-created wetlands in the Palouse Region and wetland- and landscape-level features, they have not specifically examined amphibian use of newly created wetlands. In particular, the influence of wetland age and within-wetland vegetation on amphibian establishment remains relatively unknown in this region. Such information can provide guidelines for future wetland design. Ongoing riparian and wetland restoration projects within the Palouse Region resulted in the creation of several wetlands between 1995 and 2003, which provide an opportunity to evaluate factors influencing new and relatively recently created wetland use by native amphibians. Our specific objectives were to: (1) document the use and reproduction of native pond-breeding amphibians in newly created wetlands; (2) compare the relative importance of wetland- and landscape-level factors influencing amphibian occupancy of these wetlands for reproduction; and (3) compare our results across species.

Materials and Methods

Study site.—We conducted this study within and around the city of Moscow, Idaho, USA (46.73°N, 117.00°W), in western Latah County on the eastern edge of the Palouse bioregion (Bailey 1995). Prior to European settlement, much of the Palouse was dominated by native grasses including Idaho Fescue (*Festuca idahoensis*) and Bluebunch Wheatgrass (*Elytrigia spicata*; Black et al. 1998). Aquatic amphibian breeding habitat on the Palouse prior to European settlement probably consisted of perennial and intermittent streams, ephemeral wetlands, wet meadows, and beaver ponds (Black et al. 1998). During the early 1900s, approximately 94% of the native grasslands and 97% of the native wetlands in the Palouse were converted into agricultural areas for crops, hay, or pasture (Black et al. 1998).

We surveyed 33 wetlands that were created by the Palouse-Clearwater Environmental Institute (PCEI) as part of 13 wetland or streamside restoration projects (Fig. 1). Wetland age ranged from 2–11 y (median age = 3 y). All wetlands were within approximately 5.5 km of the center of Moscow. Specifically, 23 wetlands (nine projects) were within the Moscow city limits and 11 wetlands (three projects) were approximately 1.5–3.8 km beyond the Moscow city limits.

Conditions prior to the creation of these wetlands included a degraded streambed, low vegetation diversity, and exotic invasive plants. Each of the 13 projects included multiple palustrine wetlands (mean = 3.46, range of values, 1–11) that were excavated (Cowardin et al. 1979). Wetland subclasses included unconsolidated shore (n = 19), emergent (n = 13), unconsolidated bottom (n = 7), and shrub-scrub (n = 1; Cowardin et al. 1979). Wetland hydroperiod classifications included ephemeral (n = 18), intermittently or semi permanently exposed (n = 18) in which water covers substrate throughout the year except during extremely dry years, and permanently flooded (n = 4), in which water covers substrate throughout the year during all years depending on

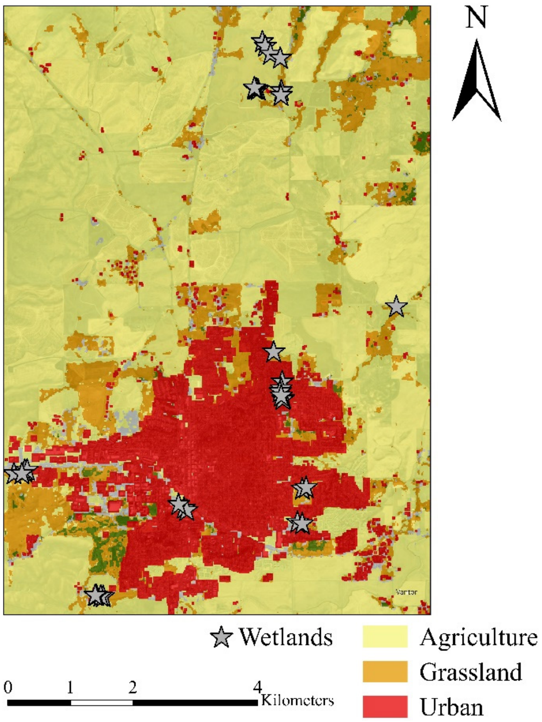

Figure 1. Map of recently created wetlands in Latah County, Idaho, USA, surveyed for amphibians during March-April 2005 with dominant surrounding land cover types. Projects are denoted by clusters of wetlands (stars). Note that there are three projects in the northeast portion of the map.

winter precipitation (Cowardin et al. 1979). Wetlands rarely exceeded 2 m in depth. Wetland vegetation included aquatic emergent species, such as Broadleaf Cattail (*Typha latifolia*), bulrushes (*Scirpus* spp.), and Idaho Sedge (*Carex idahoa*), as well as submerged terrestrial species (e.g., grasses), which comprised the majority of submerged and emergent vegetation in many wetlands.

Amphibian sampling.—We surveyed wetlands during the spring of 2005 (5 March 2005 through 23 April 2005). We surveyed for presence and reproduction of Colombia Spotted Frog *(Rana luteiventris*; SPFR*)*, Sierran Treefrog (*Pseudacris sierra*; SITF), and Long-Toed Salamander (*Ambystoma macrodactylum*; LTSA). We visited all wetlands containing standing water during our survey period except six wetlands in one project where thick vegetation largely prevented us from accessing the standing water in those wetlands. Ten wetlands were dry at the start of the 2005 surveys but filled with rainwater after the start of the survey period. We subsequently added them to the study.

We used Visual Encounter Surveys (VES), dip-netting, and funnel trapping to sample amphibians. One to three people at a time conducted VES by walking once along the entire perimeter of each wetland. During the VES, we also took dip-net sweeps along the bottom of each wetland perpendicular to the shore about every 5 m. We used collapsible minnow traps (MT4 Collapsible Trap; Nylon Net Co., Memphis, Tennessee, USA) to sample breeding adults by placing one to six traps, depending on wetland size, overnight in each wetland. Individual trapping nights were ≥ 5 d apart. We conducted two to three VES and one to three overnight trapping sessions at each wetland with fewer surveys/sessions at wetlands that were dry at the beginning of our study but subsequently filled with water. We detected reproduction (i.e., eggs or larvae) of these species much less often than adults through trapping. We therefore restricted our analyses of amphibian reproduction (i.e., detections of eggs or larvae) to data collected during VES/dip-netting surveys. We recorded the presence and species of any fish detected during our surveys and trapping.

Covariate collection.—We visually estimated the percentage of the wetland margin with emergent vegetation (e.g., cattails, bullrushes, sedges; EVEG) and submerged vegetation of any kind (e.g., emergent vegetation and submerged terrestrial grasses and forbs; SVEG) during late March or early April. We recorded wetland age (AGE) to the nearest year. We used a previously developed land cover map for the Palouse Region (Poceqicz et al. 2008) to measure characteristics of the landscape at various distances (buffers) from each wetland. We used 30, 100, 500, 1,000, and 2,000-m radius circular buffers because Goldberg and Waits (2009) found that landscape features influenced wetland occupancy in the Palouse Region by our three study species across this range of scales. We measured the proportion of each buffer that was classified as urban, agriculture, and grassland. Our goal was to measure project-level, rather than wetland-level, occupancy (see below) as a function of landscape features and our study included only 13 wetland projects. We used a Principal Components Analysis (PCA) on our 15 landscape covariates (three land covers at five spatial scales) to distill our multiple landscape covariates into a smaller number of covariates that would integrate shared variation in land cover across buffers. Preliminary analyses also indicated similar results across different buffer sizes. We used the terra package (v. 1.7-23, Hijmans 2023) in R (v. 4.0.2, R Core Team 2020) to extract Covariates.

Occupancy models.—We used multi-scale occupancy models (Mordecai et al. 2011; Nichols et al. 2008) to model amphibian occupancy while accounting for imperfect detection.

$$zi \sim \mathrm{Bernoulli}(\psi i,)$$
$$ui,j|zi \sim \mathrm{Bernoulli}(\theta i,j)$$
$$yi,j,k|ui,j \sim \mathrm{Bernoulli}(pi,j,k)$$

Because of the hierarchical nature of our data as wetlands nested within restoration projects, we modeled wetland- and project-level occupancy such that the probability of occupancy of wetland *j* (θ) was conditional on the probability of occupancy of project *i* (ψ) in which wetland *j* was located. Probability of detection (*p*) during visit *k* was therefore conditional upon wetland-level occupancy. Latent occupancy states for projects and wetlands are represented by *z* and *u* respectively.

We used the mean value of the first principal component from our landscape covariate PCA across all wetlands within a project as the sole covariate for modeling project-level occupancy. We were specifically interested in the effects of wetland age and vegetation levels on wetland-level occupancy because of the potential importance of wetland vegetation for amphibian use of recently created wetlands (Hamer 2012; Holzer 2014). Additionally, planting emergent vegetation is one means by which managers could potentially increase the suitability of newly created wetlands for amphibians. Prior to model fitting, we tested for collinearity among these three covariates using variance inflation factors (VIF; Zuur et al. 2010). Variance inflation factors among these three covariates was relatively low (AGE = 1.43, SVEG = 1.40, EVEG = 1.30) as were pairwise correlation coefficients ($r \leq 0.49$). Preliminary analyses, however, indicated that some our coefficient posteriors were sensitive to the combination of these covariates included in the model. This indicated that our model results were sensitive to the low levels of collinearity we observed, a pattern potentially exacerbated by our small sample size ($n = 33$ wetlands). We therefore used a Bayesian Variable Selection Process to first evaluate the relative support among these three covariates and then re-fit the model modeling wetland-level occupancy as a function of the best supported covariate. Specifically, we used a latent indicator variable to select one of these three covariates for inclusion in the model on each Markov Chain Monte Carlo (MCMC) iteration. We used the dcat (0.33,0.33,0.33) prior for this latent indicator variable. This approach ensured that only one of these three variables was included in the model at a time, and we used the proportion of MCMC iterations where a variable was included to identify the best-supported covariate. We then reran a final model for each species/life stage (presence or reproduction) using the single wetland-level covariate with the greatest empirical support.

Our three amphibian species initiate reproduction at different times within our study area. Within our study area, LTSA may begin reproduction as early as February (Nussbaum et al. 1983; pers. obs.) while SPFR may begin reproducing in March (Davis and Verrell 2005). Sierran Treefrogs in our study area may begin breeding later in March or April, and therefore our surveys may have covered only a portion of the SITF breeding season. We therefore treated survey date as a continuous linear covariate (1 = 1 March, 2 = 2 March, 32 = 1 April) and modeled detection probability as a function of survey date to account for temporal variation in species abundance as they arrived at wetlands for breeding. Additionally, we used data only after the date from that we first detected the presence (i.e., any life stage) or reproduction for each species to ensure that we met the assumption of site closure (MacKenzie et al. 2018). We therefore use the following initial cutoff dates for presence and reproduction, respectively: 5 March and 26 March for SPFR, 2 April and 9 April for SITF, and 5 March and 18 March for LTSA. We also modeled detection probability as a function of EVEG to account for potentially reduced detection in more heavily vegetated wetlands. For models using data from all life-stages (i.e., species presence), we included two intercepts in the detection portion of our model: one for VES/dip-netting surveys and one for trapping. We included survey date and EVEG as additive effects. We also included an additive effect of number of trap nights for trapping data to account for trapping effort (Table 1).

Model fitting.—We fit our models for each species in a Bayesian framework using JAGS (v. 4.3.0; Plummer 2003) called from the package jagsUI (v. 1.5.1; Kellner 2019; see Appendix for code). We used logistic priors for all intercepts (Logistic[$\mu = 0$, $\sigma = 1$]) following Northrup and Gerber (2018) and Gaussian ($\mu = 0$, $\sigma = 1.648$) priors for all slopes following Chandler et al. (2015) to provide a degree of regularization to our estimates. All continuous covariates were *z*-score standardized prior to model estimation.

Table 1. Linear predictors in Multi-Scale Occupancy Models used to model project and wetland occupancy (ψ and θ, respectively) of three species of pond-breeding amphibian in recently created wetlands in Latah County, Idaho, USA. Principle Component 1 (PC1) is the mean value of the first principal component across all wetlands in a given project from a principal components analysis run on all of our multi-scale landscape covariates and is positively correlated with urban landcover. Wetland Covariate refers to the wetland-level covariate (wetland age [AGE], percent wetland margin of emergent vegetation [EVEG], or percent wetland margin of submerged vegetation [SVEG]) that was best supported using Bayesian variable selection. Detection models for amphibian reproduction included two intercepts: one for surveys done using Visual Encounter Surveys (VES) and one for surveys done using trapping. Trapping surveys included an additive effect of number of trap nights to account for trapping effort.

Parameter	Linear Predictor
Project Occupancy (ψ)	$\text{logit}(\psi_i) = \beta_\psi + (\beta_{\text{PC1}} \times \text{PC1})$
Wetland Occupancy (θ)	$\text{logit}(\theta_{i,j}) = \beta_\theta + (\beta_{\text{Wetland Covariate}} \times \text{Wetland Covariate})$
Detection - Reproduction (p)	$\text{logit}(p_{i,j,k}) = \beta_p + (\beta_{\text{Survey Date}} \times \text{Survey Date}_{i',j,k}) + (\beta_{p(\text{EVEG})} \times \text{EVEG}_{i',j})$
Detection - Presence (p)	$\text{logit}(p_{i,j,k}) = ([\beta_{p(\text{Trap})} + \beta_{p\text{Trap Nights}} \times \text{Trap Nights}_{i',j,k}] \times \text{Trap}_{i',j,k}) + (\beta_{p(\text{VES})} \times \text{VES}_{i',j,k})$ $+ (\beta_{\text{Survey Date}} \times \text{Survey Date}_{i',j,k}) + (\beta_{p(\text{EVEG})} \times \text{EVEG}_{i',j})$

We ran 20,000 adaptive iterations and 20,000 burn-in iterations across three parallel Markov chains before sampling 80,000 iterations from the posterior distribution while retaining every 10th posterior sample. We visually assessed MCMC chain convergence and mixing and ensured that Gelman-Rubin statistics ($\hat{R}$) were ≤ 1.01 for all coefficient parameters (Brooks and Gelman 1998; Gelman and Hill 2006). We also report the means and 95% credible intervals (CRI) of parameter posterior distributions. Because of our small sample sizes, we were concerned with elevated Type II error and therefore did not make inferences solely from parameters whose 95% CRI excluded zero. Our Bayesian analytical framework allowed us to evaluate parameter support using the entire posterior distribution, not only the CRI. We therefore calculated posterior probability values for all covariate posteriors as the proportion of posterior samples with the same sign (positive or negative) as the posterior mean (e.g., Zylstra et al. 2019). Finally, we calculated a mean conditional wetland-level occupancy by calculating the proportion of occupied wetlands using the latent variable matrix μ for each posterior sample.

Results

The first principal component explained 59% of the variation in our land cover data and was positively correlated with urban land cover (r = 0.80–0.99) and negatively correlated with agriculture (r = -0.59, -0.92) and grassland (r = -0.32, -0.65). Covariate values ranged from -3.28 to 4.17 for each wetland (Supplemental Information Table S1). We detected SPFR reproduction in 12 (36% of total sites) wetlands, SITF reproduction in 11 (30%) wetlands, and LTSA reproduction in 14 (42%) wetlands. Mean conditional wetland-level occupancy for presence was 0.57 (95% CRI = 0.52–0.67) for SPFR, 0.59 (95% CRI = 0.55–0.73) for SIFT, and 0.54 (95% CRI = 0.45–0.64) for LTSA. For reproduction, the mean conditional wetland-level occupancy was 0.40 (95% CRI = 0.36–0.45) for SPFR, 0.48 (95% CRI = 0.30–0.76) for SITF, and 0.52 (95% CRI = 0.42–0.61) for LTSA.

Detection probability for both SPFR presence and reproduction and for SITF presence strongly increased during our survey season with a similar but weaker relationship also occurring for SITF reproduction (Figs. 2, 3, Tables 2, 3; Supplemental Information Figs. S1 and S2). In contrast, detection for LTSA presence was greatest early in the survey season while detection for LTSA reproduction was relatively insensitive to survey date (Fig. 4, Tables 2, 3; Supplemental Information Fig. S3). Detection for SPFR presence and for LTSA presence and reproduction was also greatest in wetlands with greater emergent vegetation (Fig. 4, Tables 2, 3; Supplemental Information Figs. S1 and S3). Emergent vegetation had contrasting effects on SITF detection with a negative effect on detection for SITF presence and a positive effect on detection for SITF reproduction (Fig. 3, Tables 2, 3; Supplemental Information Fig. S2).

Latent indicator variable selection showed that SVEG was the best predictor of wetland-level reproduction and detection for both SITF reproduction and presence and LTSA reproduction and presence (Tables 2, 3). The effect of SVEG was strongly positive for SITF but negative for LTSA (Figs. 3, 4; Supplemental Information Figs. S2 and S3). Latent indicator variable analyses showed that individual wetland age was the best predictor of wetland reproduction for SPFR. Age had a positive effect on SPFR reproduction and presence (Fig. 2; Tables 2, 3; Supplemental Information Fig. S1).

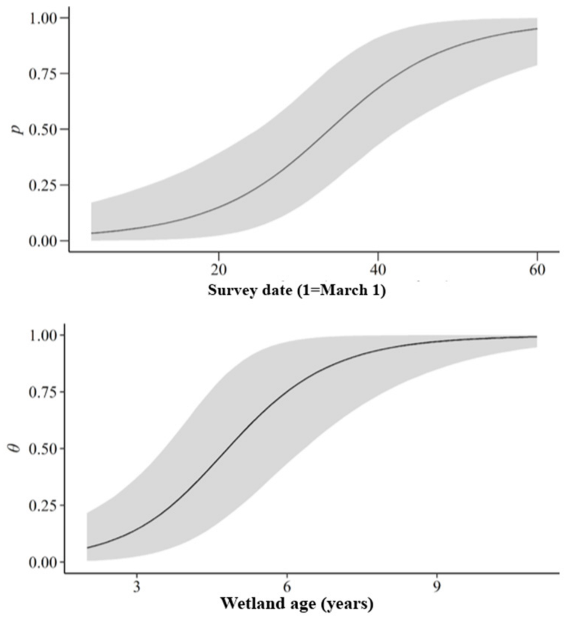

Figure 2. Predicted relationships showing the mean posterior (solid black line) and 95% credible intervals (gray area) between reproduction detection probability (*p*), wetland- (θ) and project-level (ψ) occupancy from a multi-level occupancy model of Columbia Spotted Frog (*Rana luteiventris*) reproduction in Latah County, Idaho, USA. Covariates have posterior probabilities > 0.90 and include survey date (1 = 1 March, 32 = 1 April), wetland age (years), and percentage wetland margin with emergent vegetation.

Project-level occupancy for SPFR presence was lower in wetland projects surrounded by greater urban land cover (Table 3; Supplemental Information Fig. S1). There was relatively little evidence that urban land cover affected project-level occupancy for SPFR and SITF reproduction or LTSA presence but there was a negative effect for SITF presence (Tables 2, 3; Supplemental Information Fig. S2). LTSA reproduction was also lower in wetland projects surrounded by greater urban land cover (Fig. 4, Table 2).

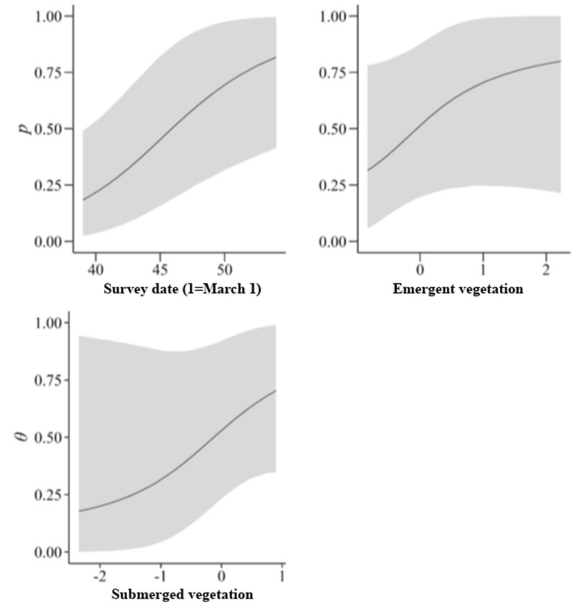

Figure 3. Predicted relationships showing the mean posterior (solid black line) and 95% credible intervals (gray area) between reproduction detection probability (*p*) from a multi-level occupancy model of Sierran Treefrog (*Pseudacris sierra*) reproduction in Latah County, Idaho, USA. Covariates have posterior probabilities > 0.90 and include survey date (1 = 1 March, 32 = 1 April) and percentage wetland margin with emergent vegetation.

Discussion

Both landscape and wetland-level features influenced amphibian use and reproduction in relatively recently created wetlands in an urban-agricultural landscape in northern Idaho. Our three study species also differed in their response to these features, likely reflecting differences in their ecology. For example, SPFR showed a consistently positive association with wetland age while LTSA and SITF were generally unassociated with wetland age. Monello and Wright (1999) also reported a positive association between SPFR and wetland age within our study area. Our results also indicated that SPFR were not strongly influenced by wetland vegetation. Therefore, the association with older wetlands is most likely not due to older ponds having more vegetation. Instead, the positive relationship between wetland age and SPFR occupancy may reflect dispersal and/or migratory behaviors. Male SPFR choose suitable sites and call to females for breeding (Licht 1969), and then often return annually to the same breeding sites (Pilliod et al. 2002). That may mean that SPFR reproduction is more likely in older wetlands that are familiar to males. The weak association between wetland age and LTSA and SITF occupancy was also consistent with results from Monello and Wright (1999). Both LTSA and SITF will readily use shallow ephemeral wetlands for breeding (Nussbaum et al. 1983; Guderryahn et al. 2016; Munger et al. 1998; Pearl et al. 2005), which may allow them to quickly colonize newly created wetlands. Guderryahn et al. (2016) found that LTSA and SITF were more likely to occur in younger wetlands in western Oregon. Our species-specific responses to wetland age resemble those from Bartelt and Klaver (2017) regarding amphibian use of recently restored wetlands in an agricultural landscape in the Midwest of the U.S. They found that another *Pseudacris* species,

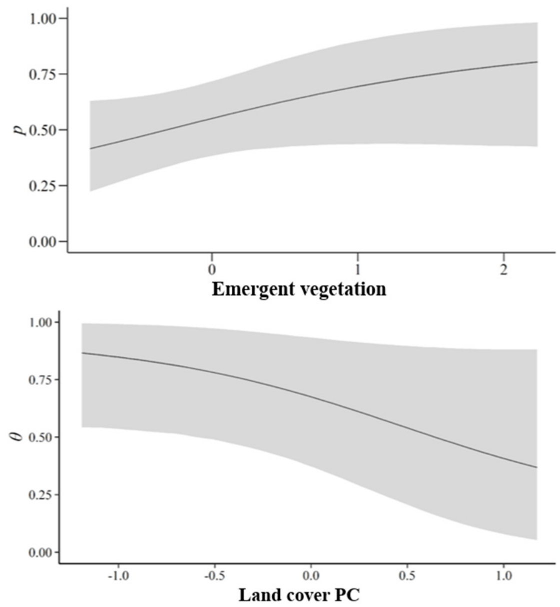

Figure 4. Predicted relationships showing the mean posterior (solid black line) and 95% credible intervals (gray area) between reproduction detection probability (p) and project-level (ψ) occupancy from a multi-level occupancy model of Long-Toed Salamander *(Ambystoma macrodactylum)* reproduction in Latah County, Idaho USA. Covariates have posterior probabilities > 0.90 and include survey date (1 = 1 March, 32 = 1 April), wetland age (years), and percentage wetland margin with emergent vegetation.

the Boreal Chorus Frog (*P. maculata*), colonized wetlands within one year, whereas another ranid frog, the Northern Leopard Frog (*Lithobates pipiens*), took up to three years to colonize wetlands.

Our results were less consistent with respect to the influence of urbanization on the occupancy of our species although SPFR and SITF presence and LTSA reproduction were negatively associated with urbanization. Previous studies have reported negative relationships between amphibian diversity and reproduction and urban environments across a diversity of landscapes (Richter and Azous 1995; Lehtinen et al. 1999; Pellet et al. 2004; Rubbo and Kiesecker 2005; Gagne and Fahrig 2007). Urbanization may negatively affect amphibians through multiple mechanisms including loss of terrestrial habitats (Semlitsch 1998), altered water flow regimes from impervious surfaces (Richter and Azous 1995; Willson and Dorcas 2003), and a reduction of ecological connectivity (e.g., through road mortality; Laan and Verboom 1990; Hels and Buchwald 2001; Goldberg and Waits 2010). The negative relationship between urban land cover and LTSA and SPFR reproduction in our study may reflect their use of both aquatic and terrestrial habitats across life-history stages (Nussbaum et al. 1983; Pilliod et al. 2001; Pilliod and Fronzuto 2005). In our study, wetlands with minimal amounts of urbanization were surrounded by agricultural landscapes; however, previous studies in our study region have found negative associations between both LTSA and SPFR and agricultural landscapes (Monello and Wright 1999; Goldberg and Waits 2009). These studies spanned a greater diversity of landscape compositions than our study, which likely explains this discrepancy with our results. Indeed, our results are at least partially consistent with the broader pattern of negative associations between LTSA and SPFR and increasing landscape disturbance. Goldberg and Waits (2009) also found that SITF were positively associated with wetlands in more open environments, including agricultural landscapes.

Submerged wetland vegetation had a negative effect on LTSA presence, but little effect on their reproduction occupancy. Indeed, we failed to detect LTSA in a project with five 8-y-old heavily vegetated wetlands, both during 2005 and during preliminary field work in 2004, although LSTA were detected in some of these wetlands during 2006 (unpubl. data). These weak or negative relationships with wetland vegetation contrast with the results of previous studies showing positive associations between LTSA reproduction and wetland vegetation (Monello and Wright 1999; Pearl et al. 2005). We do not think our results are an artifact of poor detection of LTSA in vegetated wetlands, as detection probability was higher in more vegetated wetlands and our detection rates were relatively high for LTSA. It is possible that associations with unmeasured covariates were driving the negative relationship between vegetation and LTSA occupancy, although additional research is needed to evaluate this hypothesis.

Submerged vegetation had positive effects on SITF presence and reproduction. Interestingly, Munger et al. (1998) found that SITF were positively associated with emergent and submerged vegetation but negatively associated with woody vegetation. As previously mentioned, emergent vegetation had little effect on SPFR presence and reproduction. This contrasts with other studies reporting positive SPFR associations with wetland vegetation for breeding (Licht 1971; Munger et al. 1998; Monello and Wright 1999; Greene and Funk 2009) and a study reporting that oviposition sites were clustered around vegetated areas (Pearl et al. 2007). One possible explanation for this discrepancy is SPFR responded more strongly to other forms of submerged vegetation, yet our more

Table 2. Posterior means, 95% credible intervals (CRI), and posterior probabilities (PP) of covariates from a multi-level occupancy model for amphibian reproduction (i.e., detection of eggs or larvae) in recently created wetlands in Latah County, Idaho, USA. The covariate for wetland-level occupancy was chosen with latent indicator variable selection. Principle Component (PC)1 is the mean value of the first principal component across all wetlands in a given project from a Principal Components Analysis run on all of our multi-scale landscape covariates and is positively correlated with urban landcover. Posterior probabilities are the proportion of posterior samples with the same sign (positive or negative) as the posterior mean. Posterior probabilities greater than 0.90 are boldfaced.

Parameter	Covariate	Mean	95% CRI	PP
Long-Toed Salamander (*Ambystoma macrodactylum*)				
Detection (p)	Day	0.04	-0.62, 0.71	0.55
	Emergent vegetation	0.68	-0.14, 1.56	**0.95**
Wetland Occupancy (θ)	Submerged vegetation	-0.90	-3.26, 1.08	0.80
Project Occupancy (ψ)	PC1	-1.27	-2.93, 0.32	**0.95**
Sierran Treefrog (*Pseudacris sierra*)				
Detection (p)	Day	1.49	0.32–3.08	**1.00**
	Emergent vegetation	1.20	-0.42, 3.42	**0.90**
Wetland Occupancy (θ)	Submerged vegetation	1.10	-0.74, 3.16	**0.92**
Project Occupancy (ψ)	PC1	-0.41	-2.53, 1.84	0.66
Colombia Spotted Frog (*Rana luteiventris*)				
Detection (p)	Day	1.89	0.79–3.25	**1.00**
	Emergent vegetation	0.32	-0.62, 1.23	0.76
Wetland Occupancy (θ)	Age (years)	3.07	1.48–5.19	**1.00**
Project Occupancy (ψ)	PC1	-0.51	-2.65, 1.68	0.69

comprehensive submerged vegetation covariate showed an equally weak to moderate association with SPFR occupancy. Notably, the median value for SVEG was 0.90, suggesting that our wetlands may have been sufficiently vegetated for use by SPFR and/or had insufficient variation to detect a statistical relationship with SPFR occurrence.

Amphibians appeared to colonize wetlands in this study relatively quickly. Reproduction was observed in many wetlands 2 y after their creation, and all three amphibian species were found breeding in 2- and 4-y-old wetlands. These results are consistent with those found by other studies, where amphibians were observed reproducing in constructed or restored wetlands within 1 y of their creation (Pechman et al. 2001; Petranka et al. 2007; Ammon et al. 2003; Vasconcelos and Calhoun 2006; Bartelt and Klaver 2017). Two anecdotal observations from our study, however, suggest that some minimal level of wetland vegetation in our newest wetlands may have facilitated amphibian colonization. In one of our 2-y-old wetlands that had very low levels of emergent vegetation, the only evidence of SITF reproduction we observed was a single egg clump laid on one of our traps. This may suggest that reproductive SITF were present at the site but that vegetation for oviposition was lacking. Another 2-y-old wetland had been largely devoid of vegetation the previous year (2004) and no amphibians had been detected (unpubl. data). During the summer of 2004, this wetland received several plantings of cattails and bullrushes, and in 2005 we detected SPFR (albeit no SPFR reproduction). Adding vegetation to new wetland projects may therefore help facilitate quicker wetland occupancy, particularly reproduction, by amphibians. The negative associations we found between some species (i.e., LTSA) and wetland vegetation, however, indicates that more research is needed to understand species-specific responses to wetland vegetation in these newly created wetlands.

Multiple covariates influenced detection across our study species. Sierran Treefrog and SPFR detection increased during our study likely reflecting the relatively later breeding phenology of these species compared to LTSA (Nussbaum et al. 1983; Fukumoto and Herrero 1998; Davis and Verrell 2005; Pearl et al. 2005). Throughout the Pacific Northwest of North America, LTSA are often the first pond-breeding amphibians to breed and may lay eggs when ice is still present (Nussbaum et al. 1983; Fukumoto and Herrero 1998). Detection of eggs or larvae was positively, albeit variably, associated with emergent

Table 3. Posterior means, 95% credible intervals (CRI), and posterior probabilities (PP) of covariates from a multi-level occupancy model for amphibian presence (i.e., detection of any life stage) using visual encounter surveys and dip-netting (VES and DN, respectively) and aquatic funnel trapping (Trapping) in recently created wetlands in Latah County, Idaho, USA. The covariate for wetland-level occupancy was chosen with latent indicator variable selection. Principle Component (PC)1 is the mean value of the first principal component across all wetlands in a given project from a principal components analysis run on all of our multi-scale landscape covariates and is positively correlated with urban landcover. Posterior probabilities greater than 0.90 are boldfaced. Covariates marked with asterisks (*) are detection probabilities estimated with all other covariates held constant at their means.

Parameter	Covariate	Mean	95% CRI	PP
Long-Toed Salamander (*Ambystoma macrodactylum*)				
Detection (*p*)	VES/DN*	0.52	0.37–0.67	–
	Trapping*	0.28	0.07–0.68	–
	Trap nights	0.60	-2.27, 3.39	0.66
	Day	-0.33	-0.82, 0.14	**0.92**
	Emergent vegetation	0.43	-0.19, 1.06	**0.91**
Wetland Occupancy (θ)	Submerged vegetation	-1.42	-3.75, 0.54	**0.92**
Project Occupancy (ψ)	PC1	-0.72	-2.44, 1.14	0.81
Sierran Treefrog (*Pseudacris sierra*)				
Detection (*p*)	VES/DN*	0.56	0.37–0.74	–
	Trapping*	0.29	0.09–0.62	–
	Trap nights	0.41	-2.56, 3.39	0.61
	Day	0.27	-0.25, 0.80	0.84
	Emergent vegetation	-0.44	-1.04, 0.15	**0.93**
Wetland Occupancy (θ)	Submerged vegetation	1.29	0.16–2.64	**0.99**
Project Occupancy (ψ)	PC1	-1.36	-3.16, 0.30	**0.95**
Colombia Spotted Frog (*Rana luteiventris*)				
Detection (*p*)	VES/DN*	0.44	0.29–0.59	–
	Trapping*	0.56	0.21–0.87	–
	Trap nights	-0.15	-2.92, 2.64	0.54
	Day	0.67	0.22–1.17	**1.00**
	Emergent vegetation	0.81	0.36–1.28	**1.00**
Wetland Occupancy (θ)	Age	1.51	0.04–3.19	**0.98**
Project Occupancy (ψ)	PC1	-1.33	-3.14, 0.60	**0.93**

vegetation for all species. All species primarily deposit eggs in or on submerged vegetation, so more heavily vegetated wetlands may have provided increased opportunities to deposit eggs. Visual encounter surveys combined with dip-netting had a higher probability of detecting SITF and LTSA than trapping, suggesting that future studies can rely on VES and dip-netting which is less time-intensive than trapping. While trapping did have a higher detection rate than VES/dip-netting for SPFR presence, SPFR egg masses are easily detected due to their large size, suggesting that trapping may also be less cost effective for detecting SPFR reproduction.

We realize that there are several limitations to our study. First, our sample sizes were quite small which increased the uncertainty of our parameter estimates, although our use of Bayesian posterior probabilities allowed us to make more nuanced inferences regarding the weight of evidence for our covariates. Second, our study duration may have been insufficient to fully document the extent of SITF and SPFR reproduction across our study sites, but we accounted for temporal variation in species-specific detection rates, and we have no reason to think that prematurely truncating our survey season would bias our results. Third, our wetlands occurred in highly developed landscapes (i.e., urban or agriculture), which limits the scope of inference of our study. Fourth, we had insufficient observations of fish, particularly nonnative fish, to evaluate their effect on amphibian occupancy. Previous studies throughout the Pacific Northwest have demonstrated negative associations between our three study species and nonnative fish (Monello and Wright 1999; Pearl et al. 2005; Goldbert and Waits 2009; Guderyahn et al. 2016). We detected nonnative Bluegill (*Lepomis gibbosus*) in two wetlands. In one of these wetlands, we observed LTSA and SITF reproduction and in the second one of these wetlands we only detected the presence of SPFR. Fifth, we were unable to fully evaluate the effects of wetland hydroperiod although our three study species are known to respond to wetland hydroperiod. Many constructed wetlands (i.e., human-made ponds) are permanent, which may facilitate establishment by humans of nonnative fish to the detriment of native amphibians. Alternatively, constructed wetlands may dry before amphibians can metamorphose, and this was observed at one of our sites. Sixth, we acknowledge that other unmeasured factors, such as water quality and the distribution of other unsampled wetlands within our study area, may have influenced our amphibian detections and may be important to consider for future research. Finally, we did not resurvey the wetlands in the year following our initial survey, which would have provided a more complete picture of amphibian responses to our wetlands.

Understanding factors influencing amphibian use of human-made constructed wetlands provides insights into how to best construct new wetlands. Our study shows that constructed wetlands in developed landscapes can support amphibian establishment and reproduction within a few years of creation. Both wetland- and landscape-scale factors influenced wetland use in our study suggesting that wetlands placed in landscapes with relatively low levels of surrounding urbanization with some vegetation for oviposition sites and a sufficient hydroperiod for metamorphoses may best promote amphibian use.

Acknowledgments.—We would like to thank the many individuals who assisted with this study. Lee Anne Eareckson provided valuable advice throughout this study and helped coordinate volunteer field support. Kajsa Stromberg, Tracy Brown, and the Palouse-Clearwater Environmental Institute (PCEI) provided information on wetland restoration projects, field equipment, and helped coordinate landowner access and volunteer field support. Janet Rachlow provided some field equipment and Caren Goldberg provided some funnel trapping data. Many landowners provided access to wetlands on their property. Many individuals volunteered their time to help with field work and transportation including Ryan Burner, Eric Lewis, Sara Lynd, Ciara Cusack, Caroline Campbell, Megan Chun, Brice Cooke, Erin Morra, David Nielson, Max Pengille, Leslie Penticoff, Erik Brown, Justin Saydell, Emily Poor, Jesse Bauder, Rudy Bauder, and Carolyn Bauder. This study was funded by a Berklund Undergraduate Research Scholarship to J.M.B. and the Department of Fish and Wildlife Resources at the University of Idaho. The comments of Joseph Drake greatly improved the quality of this manuscript. This study was conducted under a permit from Idaho Fish and Game and the University of Idaho Institutional Animal Care and Use Committee. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Supplemental Information: http://www.herpconbio.org/Volume_20/Issue_3/Grinder_etal_2026_Suppl.pdf

Rollie Grinder is a Ph.D. candidate at the University of Arizona, Tucson, USA, whose research explores the vulnerability of species to climate change. She examines how temperature niche breadths and thermal tolerances relate to extinction risk, how shifting weather patterns affect life-history traits, and how human interventions may support species persistence in a warming world. (Photographed by Guiliana Fusco).

Javan Bauder is an Assistant Professor at the University of Arizona, Tucson, USA, and an Assistant Unit Leader for the Arizona Cooperative Fish and Wildlife Unit of the U.S. Geological Survey. Javan studied Prairie Rattlesnake (*Crotalus viridis*) spatial ecology for his M.S., the effects of landscape features on Eastern Indigo Snake (*Drymarchon couperi*) habitat selection, population viability, genetic connectivity for his Ph.D,, and the population dynamics of furbearing mammals in Illinois during his postdoctoral research. His current research focuses on wildlife spatial, habitat, population, and landscape ecology to inform wildlife management and conservation across taxonomic groups at the level of genes, individuals, populations, and species. (Photographed by Nick Montalbano).

Charles Peterson is a Professor Emeritus of Zoology in the Department of Biological Sciences at Idaho State University and the Affiliate Curator of Herpetology for the Idaho Museum of Natural History, USA. His research interests include the spatial, physiological, and conservation ecology of amphibians and reptiles. Most of his work has focused on amphibian and reptile populations in the northern Intermountain West. Charles is currently working on amphibian monitoring in southeastern Idaho and community science projects using the iNaturalist mobile application to document the distribution and activity of amphibians and reptiles in Idaho and the Greater Yellowstone Area. He also is using place-based photography exhibits to promote the appreciation and conservation of amphibians and reptiles. (Photographed by Vince Cobb).

Dr. Edwards O. "Oz" Garton is Professor Emeritus in the Departments of Fish and Wildlife Science and Statistics at the University of Idaho in Moscow, Idaho, USA. Oz has worked with a variety of species and systems for over three decades including Greater Sage Grouse (*Centrocercus urophasianus*), Bull Trout (*Salvelinus confluentus*), Lesser Prairie Chickens (*Tympanuchus pallidicinctus*), ungulates, and on projects examining population viability, animal movement modeling, and wildlife population estimation. He has published over 100 papers and mentored 56 graduate students and postdoctoral researchers during his career. Oz and his family live in Moscow, Idaho. (Unknown photographer).

Appendix

JAGS model and R script for modeling amphibian occupancy of anthropogenic wetlands in Latah County, Idaho. The scripts for fitting the models for Columbia Spotted Frog (*Rana luteiventris*) presence are presented as examples.

```
model{

  # Priors

  # First, specify the “fixed effects” priors
  p_b0 ~ dlogis(0,1) # Intercept for detection (p)
  p_bDAY ~ dnorm(0,0.368) # Slope for an effect of DAY
on detection
  p_bEVEG ~ dnorm(0,0.368) # Slope for an effect per-
centage of wetland perimeter with submerged vegetation
on occupancy

  # Wetland-level occupancy (theta)
  theta_b0 ~ dlogis(0,1)
  theta_bWetland ~ dnorm(0,0.368)

  # Project-level occupancy (psi)
  psi_b0 ~ dlogis(0,1)
  psi_bPC1 ~ dnorm(0,0.368) # Slope for an effect of
proportion of urban on occupancy

  # BLISS for landscape covariate -----------
  # dcat is a categorical distribution which will draw a 1, 2,
or 3 with equal probability (1/3)
  Wetland_Covs ~ dcat(c(1/3, 1/3, 1/3))

  # Loop across “i” projects
  for(i in 1:N_Projects){

    logit(mu_psi[i]) <- psi_b0 + psi_bPC1*PC1[i]

    # Use this probability to flip a coin to decide if project
“i” is occupied
    # z will be either a 0 or a 1.
    # z is what is called a “latent variable” or “unobserved
variable” because we do not
    # directly observe z, but instead are estimating z from
our data.
    z[i] ~ dbern(mu_psi[i])

    # Loop across wetlands within Project “i”
    for(k in 1:Wetlands[i]){

      # Calculate the site-specific occupancy probability
based on covariate values on the logit scale
      # and use “logit” to convert to a probability.
      # Note how we use the random intercept from each
wetland’s corresponding project.
      logit(theta_mu[i,k]) <- theta_b0 + theta_
bWetland*EVEG_SVEG_Age[i,k,Wetland_Covs]

      # Flip a coin to determine if wetland “k” is occupied
conditional upon project
      # “i” being occupied
      wetland_z[i,k] ~ dbern(theta_mu[i,k]*z[i])
        # Loop across all VES surveys for each wet-
land
      for(j in 1:last[i,k]){

        # Calculate the site- and survey-specific detection
probability based on covariate values
        # on the logit scale and then use “logit” to convert to
a probability.
        # How would you add a site-level covariate, like one
of the vegetation covariates?
        logit(p_linear[i,k,j]) <- p_b0 + p_bDAY*DAY[i,k,j]
+ EVEG[i,k]*p_bEVEG

        # Because detection is conditional upon occupancy
(z=1), multiply your detection probability
        # by “z”
        mu_p[i,k,j] <- wetland_z[i,k] * p_linear[i,k,j]

        # Now do a coin flip to determine if you detected the
species in wetland i during
        # survey j
        y[i,k,j] ~ dbern(mu_p[i,k,j]*wetland_z[i,k])

      } # Survey “j”
    } # Wetland “k”
  } # Project “i”

}


model{

  # Priors

  # First, specify the “fixed effects” priors
  p_b0 ~ dlogis(0,1) # Intercept for detection (p)
  p_bDAY ~ dnorm(0,0.368) # Slope for an effect of DAY
on detection
  p_bEVEG ~ dnorm(0,0.368) # Slope for an effect per-
centage of wetland perimeter with submerged vegetation
on occupancy

  # Wetland-level occupancy (theta)
  theta_b0 ~ dlogis(0,1)
  theta_bAge ~ dnorm(0,0.368)

  # Project-level occupancy (psi)
  psi_b0 ~ dlogis(0,1)
  psi_bPC1 ~ dnorm(0,0.368)

  # Loop across “i” projects
  for(i in 1:N_Projects){

    logit(mu_psi[i]) <- psi_b0 + psi_bPC1*PC1[i]

    # Use this probability to flip a coin to decide if project
“i” is occupied
    # z will be either a 0 or a 1.
    # z is what is called a “latent variable” or “unobserved
variable” because we do not
```

```
  # directly observe z, but instead are estimating z from
our data.
  z[i] ~ dbern(mu_psi[i])

  # Loop across wetlands within Project “i”
  for(k in 1:Wetlands[i]){

   # Calculate the site-specific occupancy probability
based on covariate values on the logit scale
   # and use “logit” to convert to a probability.
   # Note how we use the random intercept from each
wetland’s corresponding project.
   logit(theta_mu[i,k]) <- theta_b0 + theta_
bAge*Age[i,k]

   # Flip a coin to determine if wetland “k” is occupied
conditional upon project
   # “i” being occupied
   wetland_z[i,k] ~ dbern(theta_mu[i,k]*z[i])

   # Loop across all VES surveys for each wet-
land
   for(j in 1:last[i,k]){

    # Calculate the site- and survey-specific detection
probability based on covariate values
    # on the logit scale and then use “logit” to convert to
a probability.
    logit(p_linear[i,k,j]) <- p_b0 + p_bDAY*DAY[i,k,j]
+ EVEG[i,k]*p_bEVEG

    # Because detection is conditional upon occupancy
(z=1), multiply your detection probability
    # by “z”
    mu_p[i,k,j] <- wetland_z[i,k] * p_linear[i,k,j]

    # Now do a coin flip to determine if you detected the
species in wetland i during
    # survey j
    y[i,k,j] ~ dbern(mu_p[i,k,j]*wetland_z[i,k])

   } # Survey “j”
  } # Wetland “k”
 } # Project “i”
}
```