

Maximizing pond biodiversity across the landscape: a case study of larval ambystomatid salamanders

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Keywords

abundance model; *Ambystoma*; hierarchical model; military base; Missouri; Ozark.

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Editor: Nathalie Pettorelli
Associate Editor: Francesco Ficetola

Received 22 April 2013; accepted 9 October 2013

doi:10.1111/acv.12090

Abstract

Loss or alteration of natural wetland habitats is a near ubiquitous global phenomenon. In the US, legislation mandates that all lost wetland habitats be replaced; manmade wetland habitats rarely have the same structural form or ecological function as natural wetlands. In the eastern US, these manmade pond habitats often serve as water sources for wildlife, but many are also utilized by amphibians for reproduction. Understanding the features that maximize species' abundance and diversity is critical to effective management. In this study, we surveyed for ambystomatid salamander larvae at 169 manmade ponds in a military training installation. Three species were present: *Ambystoma maculatum*, *A. opacum* and the regionally endemic *A. annulatum*. We estimated larval densities in each pond in relation to landscape- and pond-level covariates. Important factors relating to larval density were forest habitat surrounding each pond, canopy cover over a pond, the number of ponds within 300 m of the focal pond, presence of fish, slope of the pond basin, hydroperiod and amount of vegetation within the pond. Density estimates for each species were best predicted by different combinations of these factors, underscoring the need to provide a range of pond habitats to promote species diversity on the landscape. Our results indicate that manmade ponds are providing a valuable reproductive resource, but that future construction of ponds on the landscape will best serve the salamander and broader amphibian community if different combinations of hydroperiod and slope are utilized.

Introduction

Globally, wetland habitats are being altered, polluted or drained, and throughout much of Europe wetland losses have exceeded 50% (Halls, 1997). Wetland habitats have been reduced by >90% across the US since colonial times (Dahl, 1990). While losses have been curtailed, freshwater forested wetlands are still being lost at a rate of approximately 51 000 ha year⁻¹ (Dahl, 2011). Mitigation and restoration of wetlands has been increasing, but the form and function of these habitats are rarely equivalent to the lost or converted wetland habitat, often occurring in the form of fishless wildlife ponds of homogeneous design (Mack & Micacchion, 2006; Shulse *et al.*, 2010). Studies have experimentally tested the characteristics of newly constructed wetlands that promote amphibian species richness and metamorph production (Shulse *et al.*, 2012), and found that shallow basin slope, vegetation and absence of fish are important features. Nonetheless, individual species responses are not uniform with regard to these pond features, and colonization of created ponds is often dependent upon the surrounding habitat features and proximity to other wetlands (Lehtinen & Galatowitsch, 2001; Shulse *et al.*, 2010).

Previous studies of ponds constructed with natural substrates have found salamanders to be rare (Mack & Micacchion, 2006; Shulse *et al.*, 2010). Further, several pond-breeding caudate species (e.g. *Ambystoma bishopi*, *A. cingulatum*, *A. californiense*, *Triturus cristatus*) are threatened or endangered. To effectively manage and protect a species, it is important to understand the habitat and landscape features that affect their distribution and abundance. Although management efforts are often focused on select species (umbrella species) with the assumption of indirect conservation of co-occurring species, rarely has a single species served as an effective indicator or management tool for other species (Caro *et al.*, 2004; Ficetola *et al.*, 2007; Branton & Richardson, 2011). For European caudates, Denoël *et al.* (2013) suggest that a wide-ranging, common species may effectively serve as an umbrella for rarer species with similar life histories. These management uncertainties leave researchers and land managers with the task of identifying local habitat and regional landscape features necessary to support a species assemblage.

In our study, we estimated the larval density of three ambystomatid salamanders (*A. annulatum*, *A. maculatum* and *A. opacum*) in ponds at Fort Leonard Wood (FLW),

MO, USA. Of particular interest was the regionally endemic and poorly studied species of management concern, *A. annulatum*. Our specific research objectives were to (1) identify within-pond as well as landscape-level factors related to larval density; and (2) assess the spatial configuration of the ponds occupied by each species. We aimed to produce meaningful recommendations for the future construction and management of ponds at a landscape scale to maximize ambystomatid abundance and biodiversity.

Methods

Study area

Sampling occurred at FLW, which is an active military training facility in the Ozark Highlands, Pulaski County, MO, USA (Fig. 1; 37.92°N, 92.17°W). FLW encompasses 24 686 ha that is 80% forested, and has an extensive road system (both paved and gravel) throughout much of the military base. Active year-round military training from all five branches of the armed forces occurs onsite. More than 500 constructed and unintentional bodies of water (i.e. tire ruts), hereafter 'ponds', exist at FLW, primarily in the form of fishless, manmade wildlife ponds (<0.04 ha). Several large (>1 ha) ponds and small lakes that are stocked with game fish also occur across the site. Tire rut ponds at FLW are

water bodies formed on unpaved roads as a result of vehicle traffic. For this study, all ponds ($n = 169$) in a 7140-ha area of the west-central portion of the base (hereafter, 'focal area') were intensively sampled. The ponds and habitat within the focal area are representative of FLW and include contiguous forest, open fields and military activities (e.g. vehicle traffic and building construction).

Study species

All three of the focal study species are generally dependent upon forested habitats and fishless ponds for reproduction (Petranka, 1998). *Ambystoma annulatum* is a species endemic to the interior highlands of the Ozark and Ouachita mountains of Missouri, Arkansas and Oklahoma, while *A. maculatum* and *A. opacum* are more widely distributed throughout the forested midwest and eastern US (Petranka, 1998). Among these three species, *A. maculatum* is the only species to breed in late winter–early spring. In contrast, *A. annulatum* and *A. opacum* both breed in autumn. Unlike most ambystomatid salamanders, *A. opacum* lay their eggs on land in dry pond basins or along pond margins (Lannoo, 2005). Because *A. annulatum* and *A. opacum* breed in the fall and overwinter within the ponds, they may act as significant predators of the spring-breeding *A. maculatum* (Urban, 2007).

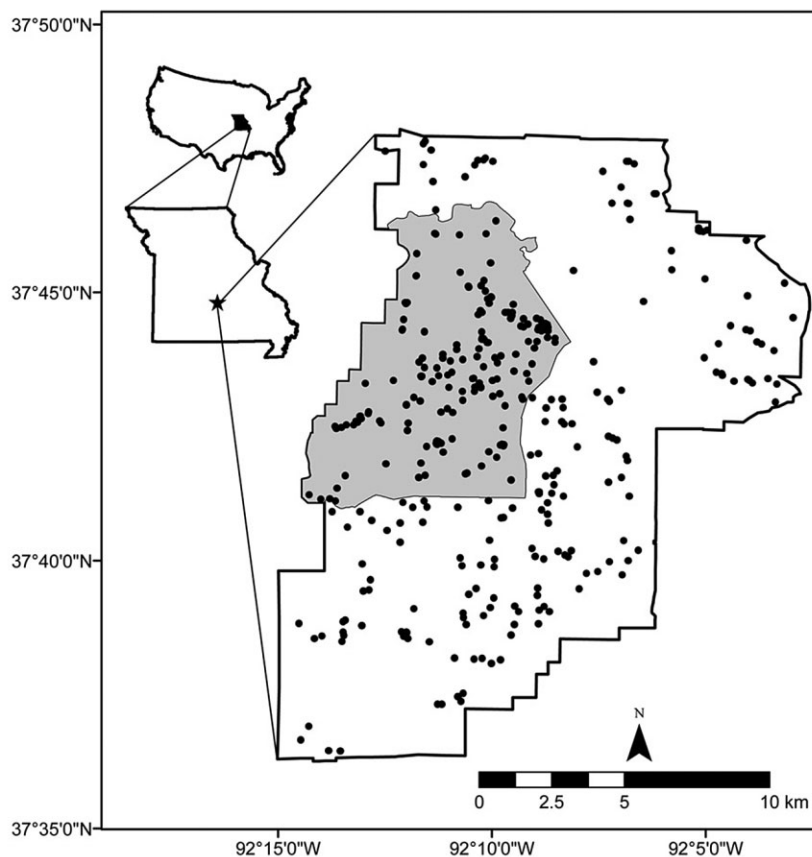


Figure 1 Map of Fort Leonard Wood, MO, USA with the focal area of this research shaded in gray. All known ponds are marked by a black dot, and all ponds within the shaded focal area were surveyed in this study.

Biotic sampling

Larval sampling of the focal area occurred at all known bodies of water during the latter third of the larval period for each species (February–March 2011 for *A. annulatum* and *A. opacum*, and May 2012 for *A. maculatum*). Generally, sites were surveyed on 3 successive days with dip-net sweeps, and most were also sampled for 3 successive nights with funnel traps. Dip-net sweeps were approximately 1.5 m in length, and included leaf litter and vegetation (Heyer *et al.*, 1994). Funnel traps (3-mm mesh; 6-mm openings; 38 × 26 × 26 cm, Memphis Net and Twine, Memphis, TN, USA) were deployed at each site when water was deep enough to cover trap openings and when site access could be guaranteed for the survey period. The number of traps was scaled to pond surface area (one per 25 m² of pond surface area; Shulze *et al.*, 2010), with a maximum of 20 traps per pond. Traps were checked daily to count the number of larvae and other aquatic animals, after which all animals were returned to the point of capture. The number of dip-net sweeps per pond (40 × 35-cm dip-net, 3.2-mm mesh) was scaled identically to funnel traps. Trap deployment and dip-net sweeps occurred within 2 m of the shoreline. Trapping and dip-netting occurred in all aquatic habitat types present (e.g. cattails, emergent grass, no vegetation) to minimize bias in selection of sampling locations. Some ponds were precluded from funnel trapping due to water depth or other logistical constraints, and only dip-net sweeps were performed at those sites ($n = 19$). On average, each pond was sampled 2.77 days (± 0.04 standard error) in each sampling round. Larval salamanders were identified based on date of sampling and body and chin pigmentation (Trauth, Robison & Plummer, 2004). Water temperature was recorded in the shade 1 m from the bank at 2 cm below the water surface at each pond on every day that sampling occurred.

Abundance and life stage of other pond community members were recorded as they occurred in dip-nets and funnel traps. In particular, the abundance of predaceous invertebrates (e.g. odonates, dytiscid beetles, crayfish, leeches, naucorids, corixids), fish, other vertebrate predators (e.g. snakes, turtles), other caudates (*Notophthalmus viridescens*) and anurans (*Rana* spp. and *Bufo* spp.) were all recorded. For our analyses, we used the number of predatory invertebrate species as a measure of predator richness (Table 1).

Habitat sampling

Abiotic and physical habitat components of each pond were measured in the summer of 2012. Canopy closure was estimated using a spherical densitometer (Forestry Suppliers, Jackson, MS, USA) during full leaf-out at the four cardinal directions along pond margins. Within-pond aquatic vegetation and habitat complexity were assessed as the percentage of the surface area that was covered by different habitat features, including down trees and vegetation (e.g. cattails, lily pads, emergent grasses). Slope of the pond basin was quantified by taking depth measurements at 1- and 2-m

distances from the shoreline and averaged for the pond. When values were not explicitly known or could not be calculated (e.g. slope of a dry pond), we used mean imputation to assign a value. The age of most ponds was obtained from FLW Natural Resources Division; for many ponds an exact year, and in other cases to within the correct decade based on past aerial photographs (K. Lohraff, pers. comm.). Hydroperiod was assigned into three categories: ephemeral (dries every year), seasonal (dries in drought years) and permanent (never dries). These categories were assigned based on visits to all ponds that occurred approximately every other month, and from historical knowledge of the area (K. Lohraff, pers. comm.). We also calculated landscape-level statistics for each pond. The per cent forest within 300 and 1000 m, pond density within 300 m, and distance to forest were all derived from the 2005 land use–land cover layer (<http://msdis.missouri.edu>) using Arc GIS 9.3 (ESRI, Redlands, CA, USA).

Analysis

Prior to analysis, we listed all environmental, habitat and sampling factors hypothesized to affect larval detection and abundance (Table 1). If two covariates had a Pearson's correlation $r \geq 0.65$, one of the two variables was retained for future analysis. Count data from larval surveys were analyzed using binomial mixture models (Royle, 2004). These models require population closure during the sampling period, an assumption likely satisfied in our study since surveys of a pond occurred over a span of 4 days or less. We chose to model larval abundance using binomial mixture models because they allow for the estimation of species' abundance as a function of site-level covariates, while accounting for imperfect species detection (Royle *et al.*, 2007). By accounting for variable detection among sites and surveys, we reduce the bias in our abundance estimate to more accurately describe larval abundances within ponds as they relate to environmental covariates (Royle, 2004; Kéry & Schmidt, 2008). Because multiple traps and (or) dip-net sweeps were used at each pond, we divided pond area by the number of traps or dip-net sweeps, and used this value as an offset to scale our abundance estimates. In doing so, our binomial mixture models produced density estimates, rather than abundance estimates, in the form of larvae per square meter.

We analyzed our models in a Bayesian hierarchical framework using JAGS (v. 3.3.0; Brossman *et al.*, 2012), executed through R (R Core Team, 2013) using the R package *R2jags* (Su & Yajima, 2012). Prior to modeling, all covariates were scaled and centered. Uninformative priors were fit to all estimated parameters using a normal distribution with a mean of zero and variance of 10^4 . Posterior summaries were based on three Markov chains, each run for 750 000 iterations and thinned at a rate of 250 following a burn-in of 250 000 iterations, which resulted in approximately 3000 samples of the posterior distribution for each estimated parameter. All *a priori* detection and abundance parameters were included in all models for each species with

Table 1 Summary of landscape and pond parameters assessed in this study

Parameter	Variable type	Data range	Rationale	Sources
Abundance model				
Fish	Presence/absence	Binary 1/0	Fish negatively influence amphibian reproduction, survival, abundance and species richness	Sexton, Phillips & Routman, 1994; Porej, Micacchion & Hetherington, 2004; Werner <i>et al.</i> , 2007; Shulse <i>et al.</i> , 2010
Structure	Percentage of pond with vegetation	36 (0–100)	Vegetation provides breeding substrate and refuge from predators	Madison & Farrand, 1998; Shulse <i>et al.</i> , 2010; 2012
Hydroperiod	Categorical (ephemeral, seasonal, permanent)	Categorical 1–3	Hydroperiod is a critical determinant of survival to metamorphosis and breeding population size	Semlitsch & Wilbur, 1988; Baldwin <i>et al.</i> , 2006
Canopy	Pond average (linear and quadratic)	38 (0.00–96.00)	Larval survival and breeding population size is greater in closed-canopy ponds	Baldwin <i>et al.</i> , 2006; Earl <i>et al.</i> , 2011
Predator richness	Number of invertebrate predator species	5.45 (0.00–12.00)	Larval mortality increases with predators, and predator richness is correlated to abundance	Relyea, 2007; Rannap <i>et al.</i> , 2009
Ponds within 300 m	Count	8.5 (1–27)	Connectivity of ponds is a predictor of salamander occupancy	Cosentino, Schooley & Phillips, 2011
Forest within 300 m	Per cent of buffer area	65 (1–100)	Salamanders abundance is strongly affected by the presence of forests in core terrestrial habitat	Semlitsch & Bodie, 2003; Porej, Micacchion & Hetherington, 2004; Shulse <i>et al.</i> , 2010
Forest within 1 km	Per cent of buffer area	72 (15–100)	Habitat within 1 km is a better predictor of salamander occurrence	Charney, 2012
Distance from forest	Euclidean distance (m)	43 (0–260)	Juvenile and adult ambystomatid salamanders have higher survival in forested habitat	Rothermel & Semlitsch, 2006
Pond age	Years	27 (4–75)	Ambystomatid salamanders are hypothesized to prefer mid- to late-succession ponds	Birx-Raybuck, Price & Dorcas, 2010
^a Presence of <i>A. annulatum</i> and/or <i>A. opacum</i>	Presence/absence	Binary 1/0	<i>A. annulatum</i> and <i>A. opacum</i> may act as a fish-like predator that <i>A. maculatum</i> avoid	Urban, 2007
Slope	Change in depth cm m ⁻¹	0.151 (0.00–0.42)	Shallow littoral zones are a predictor of amphibian richness, and may provide breeding sites and refuge from predators	Walls, 1995; Porej & Hetherington, 2005
Detection model				
Date	Julian date	–	Larval activity patterns may change throughout the sampling season	Personal observation
Temperature	Degrees Celsius	8.35 (0.50–20.00)	Larval activity may be affected by water temperature	Almeida, 2010; Mott & Sparling, 2010
Method	Dip-net or minnow trap	–	Efficacy of method may vary with larval vagility	Denton & Richter, 2012
Per cent cattail	Per cent of pond with cattails	10 (0–95)	Dip-net sweeps were potentially less effective in highly structured ponds	Personal observation
Slope	Change in depth (cm m ⁻¹)	0.151 (0.00–0.42)	Dip-net sweeps were potentially less effective in steep ponds	Personal observation

^aParameter only included in *A. maculatum* abundance model.

the exception of the presence of *A. annulatum* or *A. opacum*. This parameter was only included in the *A. maculatum* density model because these species may act as predators to reduce the abundance of *A. maculatum* (Urban, 2007). We have no reason to suspect that *A. annulatum* and *A. opacum* significantly affect the abundance of one another. Models were fit to Poisson, zero-inflated Poisson and Poisson-log-normal distributions (Millar, 2009; Kéry & Schaub, 2012).

Additionally, we fit Poisson models with a site-survey random effects error term in the detection model to account for unexplained variation in detection (Kéry *et al.*, 2009; Kéry & Royle, 2010). Model convergence was assessed using the Gelman–Rubin statistic (Rhat; Gelman *et al.*, 2004). Posterior predictive assessment of model fit was done using a Bayesian *P*-value as well as a chi-squared discrepancy measure (Gelman, Meng & Stern, 1996; Kéry, 2010);

the model that best fit our data based on these measures was used for further inference. From each model we calculated the mean and 95% credible interval for all model parameters, as well as the latent density parameter at each site.

To determine if density estimates of each species were spatially clustered, we used Moran's *I* to test for spatial autocorrelation. Tests were conducted for each species at both 500 and 1000 m neighborhood sizes, and significance was assessed using 10 000 Monte Carlo simulations using the R package *spdep* (Bivand, 2013).

Results

Field surveys

A total of 169 ponds held water and were sampled for *A. annulatum* and *A. opacum* larvae from February–March 2011, and larvae were detected at 75 and 48 ponds, respectively. Fifty-one of the ponds sampled for *A. annulatum* and *A. opacum* did not have water during our May 2012 survey for *A. maculatum*, and three new ponds not surveyed in February–March were identified and included ($n = 112$). Of the 112 ponds surveyed for *A. maculatum*, larvae were detected at 53 ponds. Fish (*Gambusia* spp., *Lepomis* spp. and *Micropterus* spp.) were detected at 25 ponds. Pond-level summary statistics for the measured covariates are included in Table 1. Results below are reported as means (\pm standard deviation), unless otherwise noted.

Abundance modeling

No detection covariates were correlated, but several abundance model covariates were significantly correlated. Correlated covariate pairs included invertebrate predator richness with hydroperiod ($r = 0.75$), per cent forest within 300 m with per cent forest within 1000 m ($r = 0.91$), and per cent forest within 300 and 1000 m with distance from the forest ($r = -0.75$ and -0.69 , respectively). Of these correlated variables, we retained invertebrate predator richness and forest within 300 m for subsequent analyses. Predator richness was retained because it was a continuous rather than categorical variable, and forest within 300 m was retained to minimize the degree of spatial overlap of covariate estimates among ponds.

The best-fitting model for each species, based on Bayesian *P*-values and chi-squared discrepancy measures, had a Poisson-log-normal distribution and included a random effects error term in the detection model. The models fit the data well for *A. annulatum*, *A. maculatum* and *A. opacum*, respectively: Bayesian *P*-values = 0.378, 0.369 and 0.380; chi-squared discrepancy = 1.04, 1.05 and 1.05. In general, there was good correspondence between the numbers of ponds where larvae of *A. annulatum*, *A. maculatum* and *A. opacum* were detected in field surveys, and ponds where our models predicted salamanders to occur (100, 90 and 76%, respectively).

Detection of all three species was not affected by any of our measured covariates, but was significantly less than one

(Table 2). Density estimates for each species were affected by different combinations of environmental or habitat covariates at the pond and landscape levels (Table 2). At the landscape scale, the amount of forest within 300 m of a breeding pond had a significant and positive affect on the densities of all three species (Fig. 2a–c), and density of *A. annulatum* and *A. opacum* increased as the number of ponds within 300 m increased (Fig. 2d–e). Both *A. maculatum* and *A. annulatum* were largely absent from ponds containing fish (Table 2). This trend was also seen in *A. opacum*, but was not significant. *Ambystoma opacum* density was positively affected by the amount of structure within a pond basin (Fig. 2f) and decreasing slope of the pond basin (Fig. 2g); two features generally associated with temporary hydroperiods. Invertebrate predator richness within a pond, which was positively correlated with hydroperiod, had a significant and positive affect on *A. annulatum* density (Fig. 2h). Density estimates of *A. maculatum* were not affected by the presence of *A. annulatum* or *A. opacum* (Table 2), but density did increase as the canopy cover over the pond increased (Fig. 2i).

There was significant spatial autocorrelation in density estimates of *A. annulatum* at both 500 m (Moran's $I = 0.324$, P -value = 0.0155) and 1000 m neighborhoods (Moran's $I = 0.285$, P -value = 0.0169; Fig. 3b). In contrast, neither *A. maculatum* nor *A. opacum* were autocorrelated at 500- or 1000-m neighborhood sizes (*A. maculatum*: Moran's $I = 0.0719$ and 0.0753, P -values = 0.302 and 0.228; *A. opacum*: Moran's $I = 0.373$ and 0.338, P -values = 0.334 and 0.323; Fig. 3c–d). The mean nearest neighbor distance between occupied *A. annulatum* ponds was 238.5 m (± 321.5 m), while the mean nearest neighbor distance between occupied *A. maculatum* and *A. opacum* ponds was substantially greater (425.3 ± 341.2 and 363.3 ± 363.5 m, respectively). The mean distance between all ponds surveyed (occupied or not) was 170.8 m (± 196.4 m).

Lastly, we assessed the per cent overlap of pond use by each species. Reflective of the unique pond and habitat associations revealed by the abundance model, there was relatively little overlap in species' use of ponds. Of the 111 ponds used for breeding, 17% were predicted to harbor all three species. *Ambystoma annulatum* were sympatric with *A. maculatum* in 12% of ponds, and sympatric with *A. opacum* in 20% of ponds. *Ambystoma opacum* and *A. maculatum* were sympatric at 9% of the ponds.

Discussion

Our analysis of larval density within ponds provided us with unbiased estimates of covariate relationships, but even in correcting for imperfect detection, our density estimates should only be viewed as a relative index and not a precise estimate. There was extreme variability in larval counts among sampling days that was not explained by measured covariates, resulting in low detection rates for all species (Table 2). To account for this variability we fit abundance

Table 2 Parameter estimates for binomial mixture models of ambystomatid salamanders at Fort Leonard Wood, MO

	<i>A. annulatum</i>				<i>A. maculatum</i>				<i>A. opacum</i>			
	Mean	SD	2.50%	97.50%	Mean	SD	2.50%	97.50%	Mean	SD	2.50%	97.50%
Abundance model												
Intercept	-2.98	0.86	-4.46	-0.95	-3.20	1.14	-5.03	-0.55	-4.87	1.38	-7.51	-2.04
Fish	-9.23	1.79	-13.13	-6.09	-8.12	1.82	-12.12	-5.08	-2.02	1.44	-4.97	0.73
Structure	-0.32	0.34	-1.01	0.33	-0.08	0.37	-0.79	0.64	-0.96	0.45	-1.88	-0.13
Canopy	-0.38	0.42	-1.23	0.45	0.82	0.39	0.03	1.59	0.85	0.55	-0.21	1.97
Canopy ²	0.32	0.46	-0.58	1.25	0.18	0.61	-1.02	1.37	0.19	0.57	-0.91	1.34
Predator richness ^a	0.77	0.40	0.03	1.60	-0.66	0.40	-1.43	0.14	-0.55	0.53	-1.57	0.52
Ponds within 300 m	1.02	0.42	0.21	1.86	-0.07	0.42	-0.88	0.76	1.33	0.57	0.25	2.50
Forest within 300 m	0.86	0.42	0.06	1.70	1.82	0.51	0.85	2.85	2.95	0.75	1.64	4.55
Age	0.05	0.33	-0.61	0.72	-0.39	0.38	-1.16	0.37	-0.32	0.42	-1.17	0.51
Slope	0.51	0.32	-0.11	1.16	-0.80	1.13	-3.49	0.85	-4.43	2.00	-8.65	-0.82
<i>Ambystoma</i> presence	-	-	-	-	0.06	0.34	-0.56	0.74	-	-	-	-
Detection model												
Intercept ^b	-2.45	0.80	-4.61	-1.37	-3.57	0.72	-5.24	-2.37	-4.13	1.28	-6.96	-1.85
Date	0.19	0.30	-0.51	0.72	0.56	0.34	-0.10	1.25	0.15	0.45	-0.72	1.07
Temp	0.18	0.24	-0.25	0.72	0.49	0.50	-0.68	1.31	0.17	0.42	-0.65	0.98
Method	-0.06	0.49	-1.04	0.92	0.96	0.77	-0.73	2.35	-1.08	0.83	-2.72	0.54
Per cent cattail	-0.36	0.25	-0.86	0.12	0.13	0.35	-0.59	0.76	-0.17	0.36	-0.88	0.55
Slope	-0.01	0.18	-0.41	0.33	-2.42	1.47	-5.17	0.73	-0.12	1.26	-2.51	2.43

^aRepresents count of invertebrate predator species encountered during surveys.

^bFollowing a logit transformation, the mean detection estimates for *A. annulatum*, *A. maculatum*, *A. opacum* are 0.08, 0.03 and 0.02, respectively.

Bolded values did not overlap zero, and were significant for that parameter–species combination. SD, standard deviation.

models with Poisson-log-normal distribution as well as an error term in the detection models. Doing so resulted in fitting models, but at the cost of precision in our detection and density estimates. Sampling effort in this study was largely constrained by site accessibility because of military training operations, and was a tradeoff between intensive sampling of a few sites or less intensive sampling at numerous sites. Future studies could increase detection probability by conducting more surveys of each pond or by using different sampling methodologies (e.g. seining).

We found that the FLW landscape contains numerous pond habitats, but less than half harbored larval ambystomatid salamanders. Only 17% of ponds in which larvae were detected were used by all three species, and the level of overlap among species pairs ranged from 9 to 20%. Like previous studies, we found that species-specific differences in life-history traits lead to unique habitat preferences and requirements (e.g. Ficetola *et al.*, 2007), emphasizing that there is rarely a single mold for constructed ponds from which conservation and management can be based upon. Previous research has found that pond placement on the landscape as well as within-pond features such as basin slope and aquatic vegetation can have significant effects on species richness, abundance and reproductive success (Shulse *et al.*, 2010, 2012). Our results corroborate the importance of these features for ambystomatid salamanders, which have been largely absent from previous studies.

The Ozark-endemic *A. annulatum* was the most widely distributed of the three species at FLW, and was also found in the highest densities in occupied ponds. In contrast to

what might be hypothesized concerning negative effects on amphibian reproduction in relation to aquatic predators (Relyea, 2007, but see Rannap, Löhmus & Briggs, 2009; Van Buskirk, 2005), *A. annulatum* were found in the highest densities in ponds with higher invertebrate predator richness. It should be noted that predator richness was strongly positively correlated with hydroperiod. As such, we cannot say that predator richness has any direct effect on *A. annulatum*. Rather, it is more likely that predator richness served as a relevant indicator of hydroperiod, and because *A. annulatum* breeds in the fall and must overwinter in ponds, extended hydroperiod affords them the necessary time to reach metamorphosis.

Commonalities among the three species were seen with regard to forest habitat on the landscape, number of ponds surrounding the focal pond and presence of fish. All three species included in our study are generally known to be dependent on forested habitat, especially surrounding breeding wetlands (Rothermel & Semlitsch, 2006; Harper, Rittenhouse & Semlitsch, 2008; Semlitsch *et al.*, 2008). This landscape-level habitat requirement was significant for all three species. Interestingly, we only found effects of canopy cover at the pond for *A. maculatum*. Canopy cover affects the amount of leaf litter input as well as primary productivity within a pond, which can affect pond community composition and amphibian reproductive success (Earl *et al.*, 2011; Earl & Semlitsch, 2013).

Both *A. annulatum* and *A. maculatum* were nearly completely absent from ponds containing fish. Presence of fish was not a significant predictor for *A. opacum* density, but

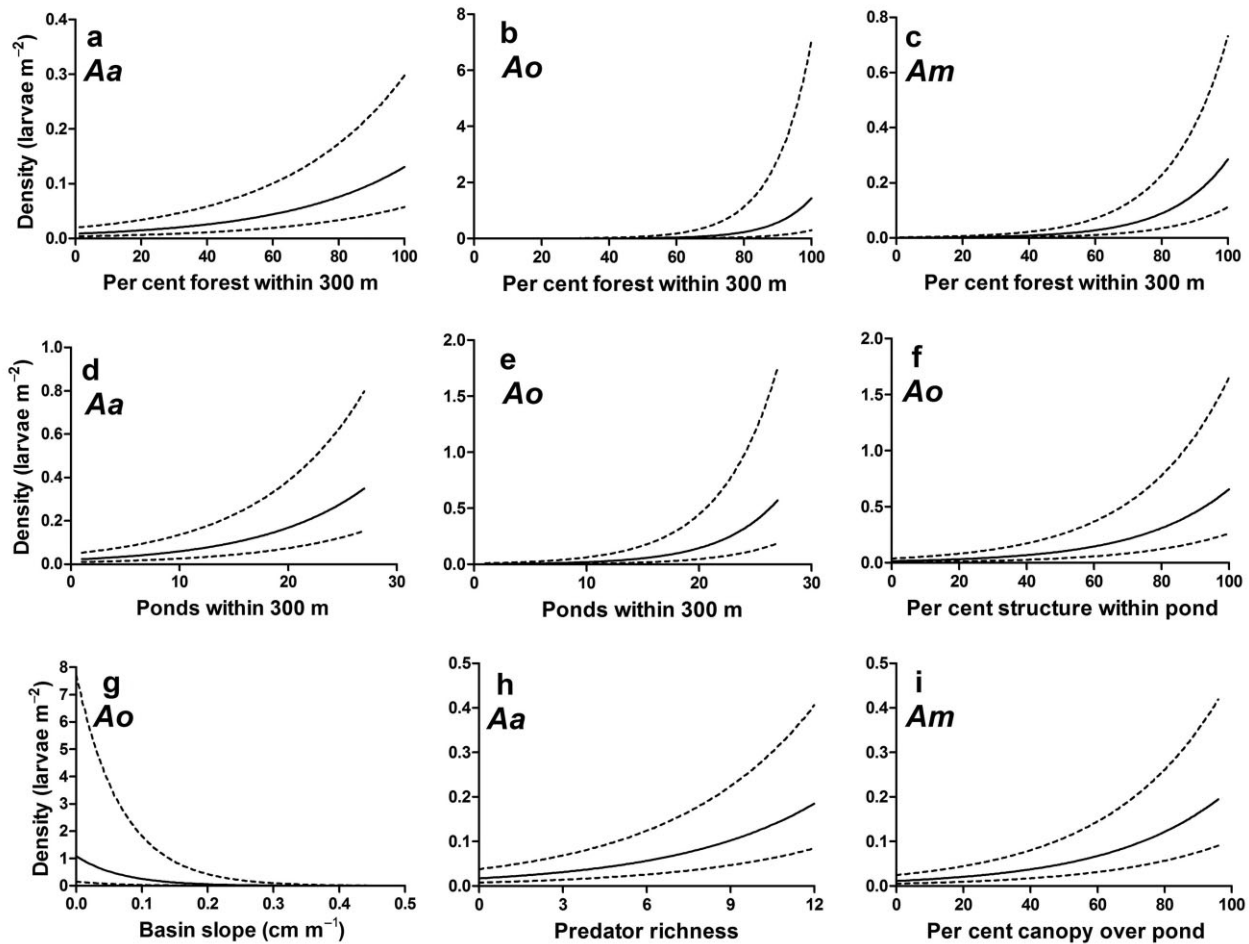


Figure 2 Estimated density of larval *Ambystoma annulatum* (Aa), *A. opacum* (Ao) and *A. maculatum* (Am) in relation to per cent forest within 300 m, the number of ponds within 300 m, predator richness, the percentage of the pond area covered by physical structure such as vegetation and coarse woody debris, the slope of the pond basin, and per cent canopy cover over the pond. Dotted lines indicate 95% prediction intervals.

this is in part likely because of their unique breeding habitat and biology. *Ambystoma opacum* deposits eggs on dry land within a pond basin; a shallow basin slope ensures that eggs will become inundated with minimal rising of the water table. Further, shallow-slope ponds tend to dry more frequently, leading to increased growth of vegetation within the pond basin, explaining why the amount of structure within a pond basin was significant for *A. opacum*. As a result, these within-pond habitat factors better explained *A. opacum* density than presence of fish.

Although the species included in our study are all forest-dependent, simply constructing a pond within the forest may not be sufficient to promote successful reproduction by some or any of these salamanders. A critical threshold of 34% forested habitat within 300 m was identified by Homan, Windmiller & Reed (2004) for the presence of *A. maculatum* in fragmented landscapes, and Denoël & Ficetola (2007) identified critical habitat thresholds for three salamander species in Europe. To maximize benefit for ambystomatid salamander (and other amphibian) diversity,

our study indicates that ponds should be placed in highly forested areas (>50% forest within a 300-m buffer), and where possible, be spatially aggregated. Maximum pond depth and slope should be minimized to prevent colonization or support of fish. Previous studies have shown that fish and basin slope in constructed ponds are critical for maximizing diversity of anurans (Shulse *et al.*, 2012), highlighting the importance of these features across amphibian taxa.

Pond-breeding amphibians are generally known to be highly philopatric and to have moderate dispersal capabilities (Berven & Grudzien, 1990; Marsh & Trenham, 2001; Gamble, McGarigal & Compton, 2007). Spatial population dynamics may also be more similar at nearby populations. Kopecký, Vojar & Denoël (2010) found that at very fine scales (<100 m), caudates breeding in tire rut habitats moved from one rut to another within a breeding season, which may serve to homogenize the distribution and density of animals. Evidence for spatial autocorrelation in density was only apparent in *A. annulatum* at both 500- and 1000-m scales. Given the significant associations of landscape- and

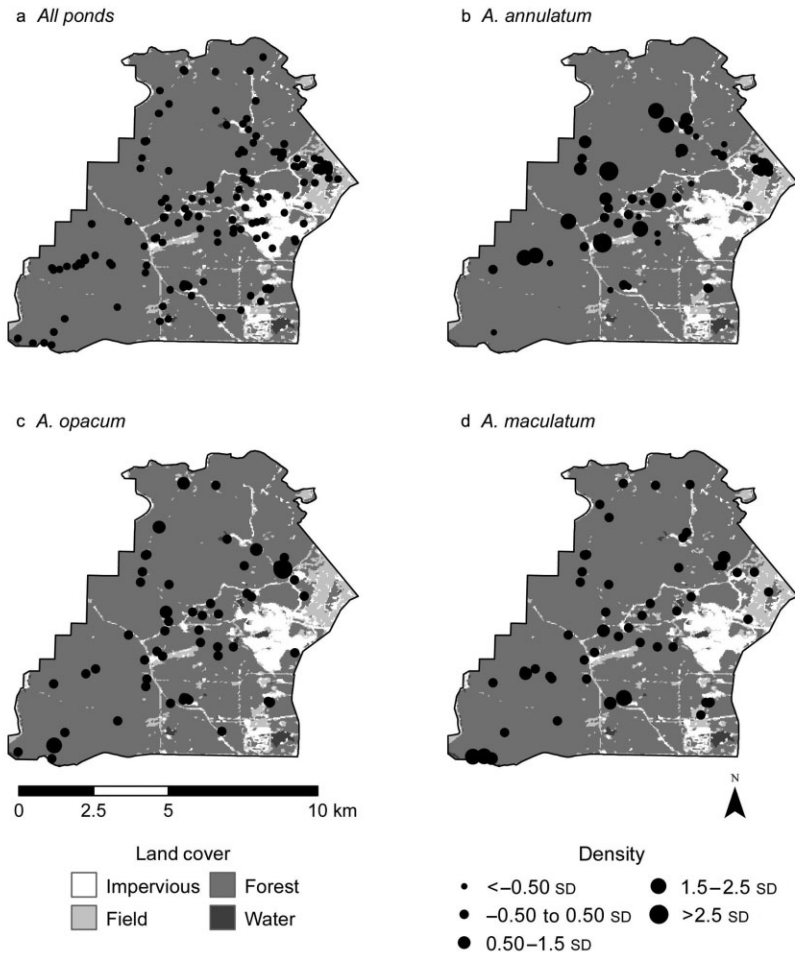


Figure 3 (a) Map showing land cover and location of all surveyed ponds on the Fort Leonard Wood landscape. (b) Location of ponds with *Ambystoma annulatum*. (c) Location of ponds with *A. opacum*. (d) Location of ponds with *A. maculatum*. Pond sizes in panels b–d are scaled to the standard deviation (SD) from the mean density estimate. Larger points represent ponds with higher than average density, smaller points have lower than average density.

pond-level covariates with density, these findings may be reflective of *A. annulatum*'s use of more permanent ponds, a common feature of manmade wildlife ponds (Shulse *et al.*, 2010). Alternatively, these patterns may be indicative of breeding pond philopatry and/or limited dispersal ability.

Because successful amphibian reproduction is closely linked with temperature and precipitation regimes that drive pond hydroperiod (Semlitsch *et al.*, 1996), which are projected to be affected by climate change (National Assessment Synthesis Team, 2000), amphibian metapopulation dynamics should be considered in future management and wetland construction (Walls, Barichivich & Brown, 2013). To foster metapopulation dynamics and colonization by dispersing salamanders, ponds should be constructed within reasonable proximity (<1000 m) to occupied breeding ponds (Jakob *et al.*, 2003; Gamble *et al.*, 2007; Kopecký *et al.*, 2010; Denoël *et al.*, 2013). Our results also indicate that clustering of ponds within 300 m can have positive effects on the local density of *A. annulatum* and *A. opacum*. In addition to placement on the landscape, structural features of each pond must also be considered. Construction of ponds within forested habitat with different combinations hydroperiod and slope will maximize breed-

ing habitat heterogeneity across the landscape, will likely promote population connectivity, and will, in turn, increase the resiliency of local populations in the face of uncertain future climate.

Acknowledgements

We would like to thank K. Lohraff for logistical help and information about ponds and J. Heemeyer for field assistance. The manuscript was greatly improved by the comments of two anonymous reviewers. This research was approved by the University of Missouri Animal Care and Use Committee (7403) and supported by the DoD Strategic Environmental Research Development Program (RC2155) and Trans World Airline Scholarship (WEP).

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1 Annotated R code to prepare data and run Bayesian binomial-mixture models using JAGS.

Appendix S2 Example data to use with the provided R code.