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Amphibian Use of Wetlands Created by Military Activity in Kisatchie National Forest, Louisiana, USA

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***Abstract*.—Constructed wetlands can provide breeding habitat for amphibians and might offset the loss of natural wetlands. Although protecting natural systems is a priority, investigating and protecting constructed wetlands should also be included in amphibian conservation efforts. We surveyed 48 small wetland pools created from military tank training (i.e., tank defilades) on Kisatchie National Forest, Louisiana, USA. We conducted surveys monthly from April to October 2012 and March to September 2013. Across both years amphibian community composition consisted of eight frog species, and the most commonly found taxa were Cajun Chorus Frogs (*Pseudacris fouquettei*), Southern Leopard Frogs (*Lithobates sphenocephalus*), and Bronze Frogs (*Lithobates clamitans*), with their larvae occurring in 85%, 81%, and 19% of pools, respectively. General linear models showed that Cajun Chorus Frog use of pools for breeding was best explained by absence of fish. The environmental factors that explained larval abundance differed between years but included absence of fish, temporary hydroperiod, open canopy, and a positive association with pH. Hydrology and conductivity best explained Southern Leopard Frog abundance. Bronze Frog presence was best explained by absence of fish and wetland slope. We did not capture other species in sufficient frequency for linear modeling, but their presence varied in response to hydroperiod, as shown by differences in similarity indices when comparing community composition between permanent and temporary pools. Our results highlight the importance of a mosaic of pool conditions and demonstrate that military activity, specifically creation of tank defilades, appears to benefit local amphibian species. Further research is required to examine larval survival and determine if any pools should be restructured to protect and create amphibian breeding habitat.**

Key Words.—Lithobates sphenocephalus, *Pseudacris fouquettei*, *Lithobates clamitans*, *Acris crepitans*, *Anaxyrus fowleri*, *Gastrophryne carolinensis*, *Hyla squirella*, *Hyla versicolor* / *chrysoscelis*

Introduction

Wetlands are important resources because of the functions they provide, including breeding and nursery habitat for many species (Mitsch and Gosselink 2007). Upland embedded wetlands, especially those that hold water seasonally, allow breeding and development of amphibians and invertebrates but deter fish and other aquatic predatory organisms (Wellborn et al. 1996; Calhoun et al. 2014; Kross and Richter 2016). These aquatic systems are an ecological asset for many species, whose life cycles require both ephemeral waters and adjacent uplands. However, because of their seasonal nature and small size, these pools are often overlooked and subsequently unprotected (Calhoun et al. 2014). Even when the destruction of these pools is noticed and mitigation occurs, the creation of new pools will often offset the wetland in area only and not necessarily in ecological function (Denton and Richter 2013). The U.S. Environmental Protection Agency (2008) has recognized that some aquatic resources such as ephemeral pools are difficult to replace, and emphasize avoidance and minimization of impact to these unique resources. Although some regulations exist requiring mitigation for destroyed or altered pools, mimicking the natural hydroperiod is often a challenge (Calhoun et al. 2014).

Hydroperiod is a critical factor in the lifecycle of amphibians. Many species native to the south-central region of North America, such as Cajun Chorus Frogs (*Pseudacris fouquettei*), require pools that dry and prevent predator colonization yet provide sufficient time for metamorphosis, while others, such as Bronze Frogs (*Lithobates clamitans*), require pools that hold water longer for maximum larval growth (Shulse et al. 2010). Having a series of pools with varying hydroperiods allows for maximum richness of species; however, creating pools that hold water for relatively specific lengths of time to meet various species ecological needs is difficult (Greenberg et al. 2015). The need to restore any loss of aquatic habitat is critical and gaining an understanding of what constitutes a suitable constructed pool is essential (Calhoun et al. 2014).

Although wetlands provide important functions, globally most historic wetlands have been altered, resulting in increased flood damage, sediment build up that chokes waterways, and a decline in biodiversity (Mitsch and Gosselink 2007; Davidson 2014). In recent years, the United States federal government has often required mitigation, or replacement of, protected wetlands (Salvesen 1994). Additionally, many entities have realized the importance of this resource and have begun wetland restoration projects for wildlife management, flood mitigation, and erosion control, and as a filtering system (Interagency Workgroup on Wetland Restoration 2003). Occasionally, wetlands are also created inadvertently by logging operations, roadway construction, or even military activity. Although artificial wetlands can provide surrogate habitat for amphibians, their suitability for individual species likely depends on incorporating habitat requirements into wetland designs (Pechmann et al. 2001; Brand and Snodgrass 2010; Denton and Richter 2013; Calhoun et al. 2014; Drayer and Richter 2016).

Because amphibians are declining globally and the primary cause of declines is habitat loss (Gardner 2001), understanding habitat requirements of species, especially the efficacy of constructed habitats, is critical to conservation and management. Many wetland-breeding amphibian species require a habitat mosaic of small breeding pools in addition to large areas of upland habitat (Semlitsch 1998; Semlitsch and Bodie 2003; Colburn 2004; Calhoun et al. 2014). At the pool-scale, unique environmental features may influence breeding of particular amphibian species (Calhoun et al. 2014). Hydroperiod strongly influences growth, survival, and community structure among larval amphibians (Rowe and Dunson 1995; Skelly 1997; Snodgrass et al. 2000; Denton and Richter 2013; Drayer and Richter 2016). Other within-pool characteristics that have been shown to affect breeding amphibian species composition include pool size (Burne and Griffin 2005), forest canopy closure over the pool basin (Caldwell 1986; Skelly et al. 1999; Skelly et al. 2002; Werner et al. 2009), and extent of shrubs and persistent non-woody vegetation (Egan and Paton 2004; Burne and Griffin 2005).

Currently, the United States military holds over 12 million ha of diverse habitat, and Fort Polk Louisiana, USA, along with U.S. Army leased land, where our study occurred, makes up approximately 75,000 ha of that property. The Sikes Act of 1960 (16 USC 670a-670o, 74 Stat. 1052, 1960) recognized the importance of natural resources on military lands and provided guidelines to protect and enhance these ecosystems while still allowing the military to train its troops. In 2013, the Sikes Act was amended to include lands leased by the military for training via cooperative agreements (Sikes Act Reauthorization Act of 2013, Subsection [b] of section 103A of the Sikes Act 16 U.S.C. 670c–1). Aquatic and terrestrial habitats required by amphibians may be directly or indirectly impacted by military installation development and training.

Areas on Fort Polk have high concentrations of small artificial pools, which were created by the U.S. Army when they excavated pits (called tank defilades) that allow tanks to drive below the surface of the ground. This creates a fighting position that protects the body of the tank with only the turret above ground and makes it less visible to the enemy along the horizon. Average length and width of tank defilades at our study site were 13.2 × 4.5 m, respectively. Tank defilades that have been abandoned for several years often hold rain water, likely due to soil compaction, and develop into potential breeding pools for amphibians. These constructed pools create a unique opportunity to study pool-scale features of amphibian breeding habitat on the same landscape that may allow us to understand the requirements for particular species. Determining how vegetation, hydrology, and other local wetland features affect different amphibian species could improve our ability to incorporate these features into future wetland construction (Denton and Richter 2013; Calhoun et al. 2014; Drayer and Richter 2016). Our objectives were to identify herpetofaunal species using tank defilade pools and determine which pool-scale characteristics are associated with presence and abundance of amphibian species.

Materials and Methods

Study site.—The Vernon Unit of Kisatchie National Forest is a 34,400-ha tract of land in Vernon Parish, Louisiana, USA, adjoining the Joint Readiness Training Center (JRTC) on the Fort Polk Army installation. The JRTC provides realistic and rigorous training that includes war game scenarios, practicing combat positions, and other role-play exercises to ready troops for real-life conditions during deployment. The Vernon Unit is leased by the U. S. Army for training and is divided into Intensive Use (IUA) and Limited Use (LUA) Areas. Throughout the 1980s, Fort Polk hosted the 5th Infantry Division, which used portions of the IUA for heavily mechanized tank training. In 2011, we identified approximately 60 tank defilades within the IUA of the Vernon Unit. Current Army regulations require that all tank defilades and other fighting positions be filled and repaired. However, in the late 1980s, regulations did not officially include leased lands, so defilades were not filled, and many now hold water (Fig. 1). These tank defilades are clustered

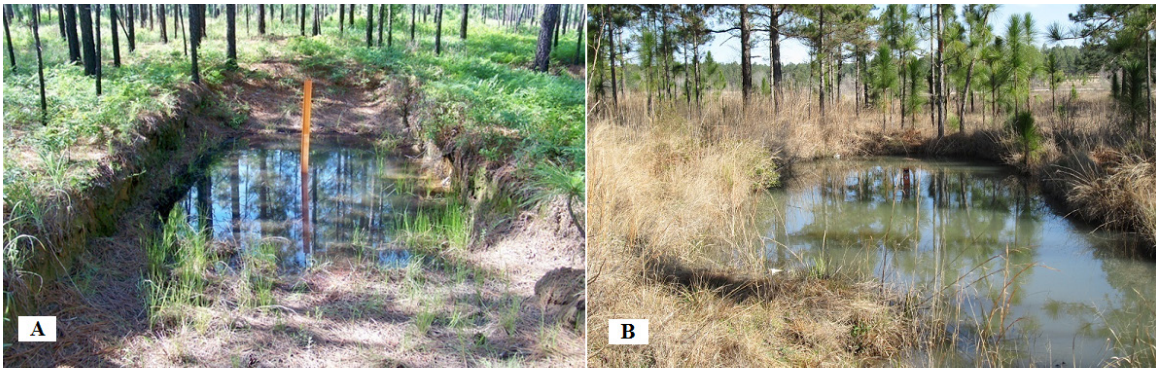

Figure 1. Two tank defilades with semi-permanent pools in August (A) and March (B) 2013. Orange carsonite stakes mark the deepest point in the pool. (Photographed by Stephen Ecrement).

within an 8-ha area located in an upland Longleaf Pine (*Pinus palustris*) ecosystem with a bluestem-herbaceous (*Andropogon* sp.) understory and is adjacent to a 121-ha, clear-cut military range. Based on aerial photos provided by the Fort Polk Environmental and Natural Resources Management Division Conservation Branch, the tank defilades on IUA property were created between 1985 and 1991.

Data collection.—In June 2011, prior to our study, we began monitoring water level in the tank defilades and determined that 48 of the 60 held water at least seasonally and could potentially support breeding by amphibian populations (Fig. 2). In 2012, access was difficult due to military training at a range adjacent to the site causing sampling to be more sporadic than in 2013. However, all pools were sampled once a month from April through early October for a total of six times each. In 2013, we divided the tank defilades into four groups of 12 and sampled each group in a random order monthly from March through September. We sampled every pool in all four groups once a month each month within a 4- to 6-d window. In both years, there was an average of 32 d between each monthly sampling event, which consisted of an amphibian survey, habitat measurements, and water quality sampling between 0600 and 1100. We used a standardized dipnetting protocol to capture larval amphibians (Dodd 2009). Prior to amphibian sampling, we measured the length and width of each pool to the decimeter using a reel tape. These measurements allowed us to calculate the surface area of an ellipse to determine the number of sweeps needed to meet a one sweep per 2 m^2 protocol. The size of the pool that day determined the number of sweeps for that month's sampling event. A sweep consisted of a surveyor extending the dipnet into the water from shore and bouncing the net along the substrate while pulling back toward the surveyor. After sampling the entire edge of the pool, each surveyor stepped further into the pool, toward the center, and repeated the dipnetting process. We spread the total number of dipnet sweeps over the entire pool in an attempt to sample the pool as evenly as possible. We counted and identified captured amphibian larvae to species, then released them on site.

We recorded water quality characteristics at each tank defilade pool prior to sampling for amphibians and recorded center surface temperature after we sampled for amphibians. We measured total percentage dissolved oxygen using a YSI 556 (YSI Environmental, Yellow Springs, Ohio, USA), pH using an Eco Testr pH2 (Oakton Instruments, Vernon Hills, Illinois, USA), and conductivity using an Accumet AP85 (Fisher Scientific, Hampton, New Hampshire, USA). We calibrated this equipment early in the day prior to sampling the entire series of 48 tank defilades.

After sampling for amphibian larvae, we measured water depth at the deepest point and 0.5 m from the edge of the water at all four cardinal directions using a meter stick. We also used these measurements to calculate tank defilade slope. We multiplied rise (water depth 0.5 m from the edge) over run (0.5 m from the edge) and averaged across all four sides of the pool. We visually estimated vegetation in each of the oblong shaped pools by sampling four 0.25 m^2 plots once annually at the midpoint of the edge of the water on all four sides and then averaged across the four samples. Using a Model-A spherical densiometer (Robert E. Lemmon, Forest Densiometers, Bartlesville, Oklahoma, USA), we recorded percentage canopy closure in the center and on all four sides of each pool, and then calculated average canopy closure (Table 1).

Because tank defilades held water for various lengths of time and we were unable to measure the exact number of days they held water, we divided hydroperiod into three hydrotypes. We created categories based on the number of months each tank defilade held water before drying over a 28-mo period (June 2011 to September 2013): Hydrotype 1 temporary (n = 25) held water a maximum of 4–8 mo each year before drying, Hydrotype 2 semi-permanent (n = 15) held water for 19–22 mo

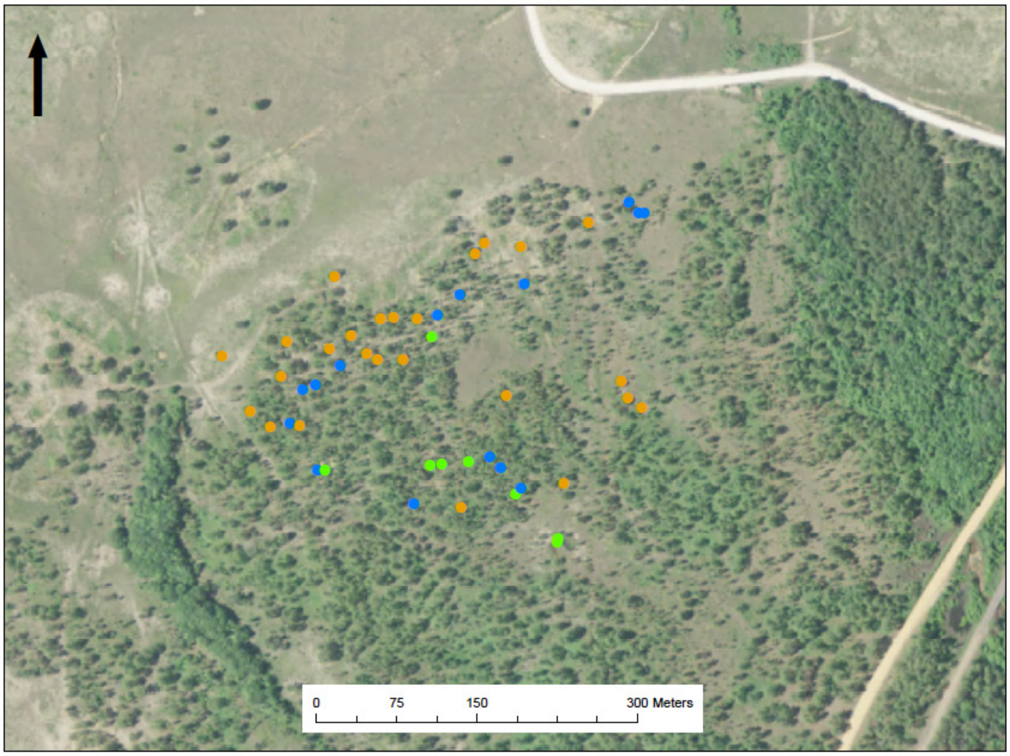

Figure 2. Aerial image of the 48 tank defilades studied from April 2012 to September 2013 and the adjacent training range on Kisatchie National Forest, which adjoins the Fort Polk military installation, in Louisiana, USA (31.042388°, -92.895007°). Orange = temporary pools (n = 25), blue = semi-permanent (n = 15), and green = permanent (n = 8). (Base photograph ®Esri, Esri, Redlands, California, USA).

before drying, and Hydrotype 3 permanent (n = 8) did not completely dry during this timeframe. In addition to water quality and habitat characteristics, we also noted the presence of fish. Although connectivity between pools did not occur during our study, it is likely that past severe weather caused flooding and connected the entire site to adjacent streams. This would explain fish colonization of separate pools typically wetted and filled by precipitation. We feel confident that we accurately measured fish presence because our study design of multiple site visits during the annual decrease in depth and surface area resulted in high detection.

Data analyses.—We determined the independence of environmental variables and their differences among hydrotypes. For each pool, we calculated the mean, maximum, and minimum of each environmental variable measured during the 2-y study period. We then calculated Spearman's rank correlation coefficients among these potential predictors of abundance. The mean of each variable was correlated to the maximum and minimum values, so we evaluated mean for correlation to all other measured variables. When pairs of predictor variables were highly correlated ($r \geq 0.7$), we removed one of the variables for modeling purposes. Our

Table 1. Mean of all samples, standard deviation (SD), maximum, and minimum of eight environmental variables collected at the 48 tank defilades in Kisatchie National Forest, Louisiana, USA, excluding when tank defilades were completely dry.

	2012				2013			
	Mean	SD	Max	Min	Mean	SD	Max	Min
Canopy Closure, %	74.98	19.59	99.00	22.00	74.98	19.59	99.00	22.00
Vegetation, %	22.11	21.12	85.00	0.00	17.27	22.43	90.00	0.00
Slope, %	0.46	0.18	0.77	0.15	0.53	0.18	0.90	0.19
Surface Area, m^2	53.33	35.59	356.76	0.88	53.53	26.33	269.70	5.95
Center Depth, cm	60.36	27.73	150.00	3.00	66.57	25.46	150.00	1.00
Temperature, °C	24.03	1.64	31.00	11.00	20.08	2.91	31.00	7.00
pH	5.78	0.25	6.90	5.20	6.60	2.45	10.10	5.10
Dissolved O_2, %	20.88	12.91	62.30	3.80	20.25	8.61	66.10	1.60

Table 2. Amphibian species observed in tank defilade pools in Kisatchie National Forest, Louisiana, USA, 2012–2013. Catch per unit effort (CPUE) is shown by Hydrotype: Temporary = 4–8 mo (n = 25), Semi-permanent = 19–22 mo (n = 15), and Permanent = did not dry (n = 8).

	Total Larvae		% of all pools		Mean CPUE ± SE; % within pool type (2012/2013)		
Scientific name	2012	2013	2012	2013	Temporary	Semi-permanent	Permanent
Lithobates sphenocephalus	1,932	990	69	71	1.27 ± 0.29; 49/56	1.74 ± 0.57; 39/35	0.18 ± 0.10; 12/09
Lithobates clamitans	20	998	4	17	0	2.78 ± 0.89; 50/50	0.81 ± 0.33; 50/50
Pseudacris fouquettei	2,403	6,756	65	79	3.31 ± 0.57; 61/58	1.23 ± 0.26; 32/31.5	0.19 ± 0.12 07/10.5
Acris crepitans	32	54	10	6	0.02 ± 0.02; 20/0	0.01 ± 0.00; 20/33	0.07 ± 0.03; 60/67
Hyla versicolor/ chrysoscelis	20	0	6	0	0.03 ± 0.03; 33/0	0.03 ± 0.02; 67/0	0
Hyla squirella	14	0	8	0	0.03 ± 0.03; 50/0	0.01 ± 0.01; 25/0	0.01 ± 0.01; 25/0
Anaxyrus fowleri	0	56	0	2	0	0	0.14 ± 0.14; 0/100
Gastrophryne carolinensis	35	0	8	0	0.02 ± 0.01; 75/0	0.08 ± 0.08; 25/0	0
*Lithobates catesbeianus**	0	0	0	2	0	0	0

*One adult was observed at one pool.

removal protocol was to first remove variables that were correlated to more than one other variable and to focus on pool morphology. We removed water temperature and center depth, resulting in eight predictor variables: hydrotype, canopy closure, emergent vegetation, fish presence, wetted surface area, slope, pH, conductivity, and dissolved oxygen (Appendix I). We ran the same analysis on each year of environmental data. We used Kruskal Wallis tests ($\alpha = 0.05$) to assess the differences in environmental variables among the three hydrotypes.

Using generalized linear models, we determined which environmental variables best predicted abundance and presence/absence of frogs. We used the monthly sampling event with the maximum number for each species within each tank defilade to avoid counting individual larvae multiple times. We divided total number of tadpoles for each species by the total number of dipnet sweeps from that sampling event to calculate a Catch Per Unit Effort (CPUE) and used that as the response variable. We performed generalized linear modeling using a Tweedie distribution with a log-link function in SPSS version 21 (IBM SPSS, Inc., Chicago, Illinois, USA). We selected the Tweedie distribution because it can accommodate discrete and continuous data as well as zeroes and because CPUE standardizes sampling effort, which results in discrete count data becoming more continuous (Shono 2008; Denton and Richter 2013). The index parameter p determines the shape of the probability distribution and can be > 1 or < 2 when using CPUE data. We selected a p of 1.5 for all models based on the highest log-likelihood value from goodness-of-fit tests of our global model (Shono 2008). We then performed reverse stepwise regression in which we began with the global model of the eight predictor variables (above) and removed the variable with the highest P-value in the model successively until all remaining variables had significance $P < 0.10$. We interpreted variables with $P < 0.05$ as significant.

We examined similarity of community composition and species turnover among the three hydrotypes. We calculated Jaccard's and Sorenson's coefficients of similarity between hydrotypes using larval presence-absence data in R version 3.3.0 (R Development Core Team, Vienna, Austria) with package VEGAN (Oksanen et al. 2011. Vegan: community ecology package. Available from http://r-forge.r-project.org [Accessed 17 December 2016]). We determined Shannon-Weiner diversity for each hydrotype using EstimateS version 9.1.0 (Colwell R.K. 2016. EstimateS Statistical Estimation of Species Richness and Shared Species from Samples. Available from http://purl.oclc.org/estimates [Accessed 17 December 2016]). We calculated species temporal turnover rate as the number of pools that changed occupancy status between the two years divided by the total number of pools used by that species.

Results

Amphibian species composition and larval abundances varied widely across the tank defilade pools. In addition to nine species of anurans (Table 2), we also observed seven reptile species at our study site (Appendix II). We confirmed larvae of eight amphibian species using 96% (46 of 48) of the tank defilade pools. Only two tank defilade pools did not contain any amphibian larvae throughout both years. We captured 4,511 tadpoles during 288 pool surveys and 8,882 as part of 336 pool surveys in 2012 and 2013, respectively. Cajun Chorus Frogs, Bronze Frogs, and Southern Leopard Frogs (*Lithobates sphenocephalus*) were the only species abundant enough to allow for regression analysis (Table 2).

Cajun Chorus Frog larval abundance was significantly explained by a positive relationship with temporary hydrotype across both years, a negative

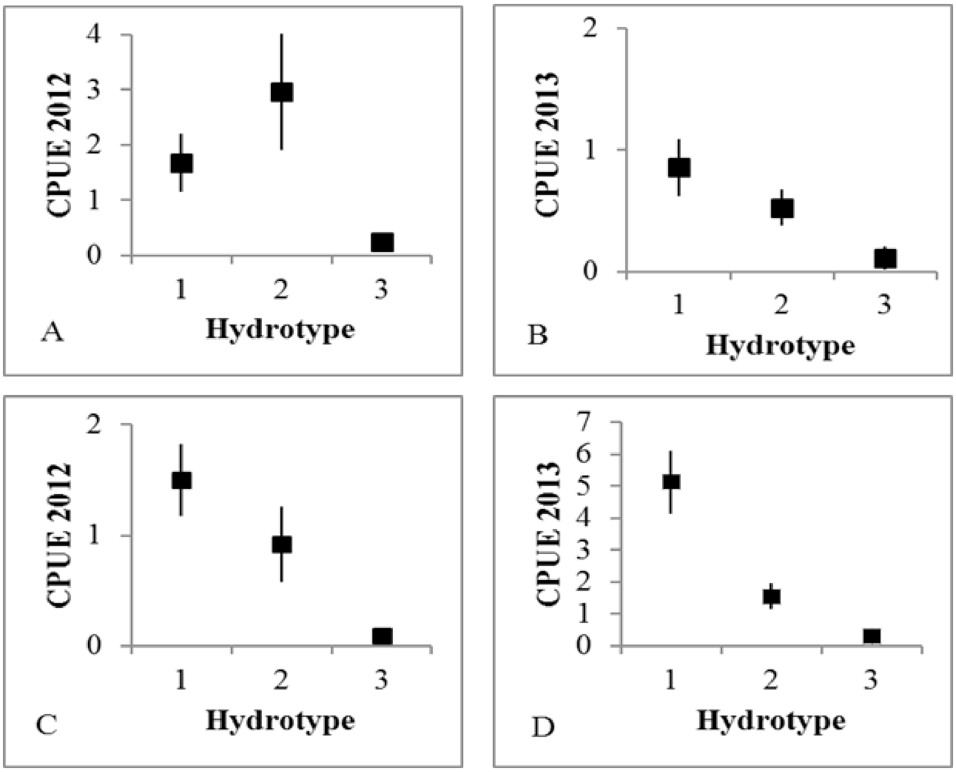

Figure 3. Southern Leopard Frog (*Lithobates sphenocephalus*; A, B) and Cajun Chorus Frog (*Pseudacris fouquettei*; C, D) mean (± SE) Catch Per Unit Effort (CPUE) shown by year (2012 and 2013) for Hydrotypes 1 (temporary), 2 (semi-permanent), and 3 (permanent).

relationship with canopy closure and fish presence in 2012, and a negative relationship with pH in 2013. Cajun Chorus Frog presence was significantly explained by fish absence both years (Table 3). There were also more larvae in pools with shorter hydroperiods in both years (Fig. 3). Southern Leopard Frog larval abundance was positively associated with temporary hydrotypes across both years (Table 3) with significantly lower abundances of larvae in permanent wetlands compared to temporary and semi-permanent wetlands (Fig. 3). Low sample size of Bronze Frogs precluded regression analysis of abundance; however, larval presence had a significant relationship with fish absence and a negative relationship with slope in 2013 (Table 3).

Multiple wetland variables were significantly different among hydrotypes, including slope (H = 28.35, $P < 0.001$), water depth (H = 33.32, $P < 0.001$), emergent vegetation (H = 19.05, $P < 0.001$), % DO (H = 17.62, $P < 0.001$), and surface area (H = 15.98, $P < 0.001$). Temporary pools had significantly shallower slopes and water depths compared to semi-permanent and permanent pools, which were steeper and deeper (Fig. 4). These patterns were similar across other variables non-significantly related to hydrotype. Pools with a temporary hydrotype were slightly warmer than pools with semi-permanent or permanent hydrotype, and surface area was smaller in pools with shorter hydrotypes (Fig. 4).

Six species captured at the study site were not included in regression analysis due to low CPUE across the pools (Table 2). Northern Cricket Frogs (*Acris crepitans*), the fourth most abundant species in our study, were slightly more abundant in permanent pools with fish present than in temporary, semi-permanent, or permanent pools without fish. Fowlers Toads (*Anaxyrus fowleri*) occurred in one permanent pool with a permanent fish population (dipnet captures = 56 tadpoles). Eastern Narrow-mouthed Toads (*Gastrophryne carolinensis*), Squirrel Tree Frogs (*Hyla squirella*) and Gray Tree Frog complex (*Hyla versicolor/chrysoscelis*) were all sparse (dipnet captures ≤ 35 tadpoles). We found one single adult male American Bullfrog (*Rana catesbeianus*) on the edge of a pool but no larvae.

Shannon-Wiener diversity, based on larvae, did not vary widely, but was higher in semi-permanent pools than permanent or temporary pools (Table 4). Similarity of communities between temporary and semi-permanent pools was high, especially when comparing temporary and permanent or semi-permanent and permanent pools (Table 4). Turnover of individual species varied among the three most common species. Southern Leopard Frogs occurred in 28 pools (58%) both years, five

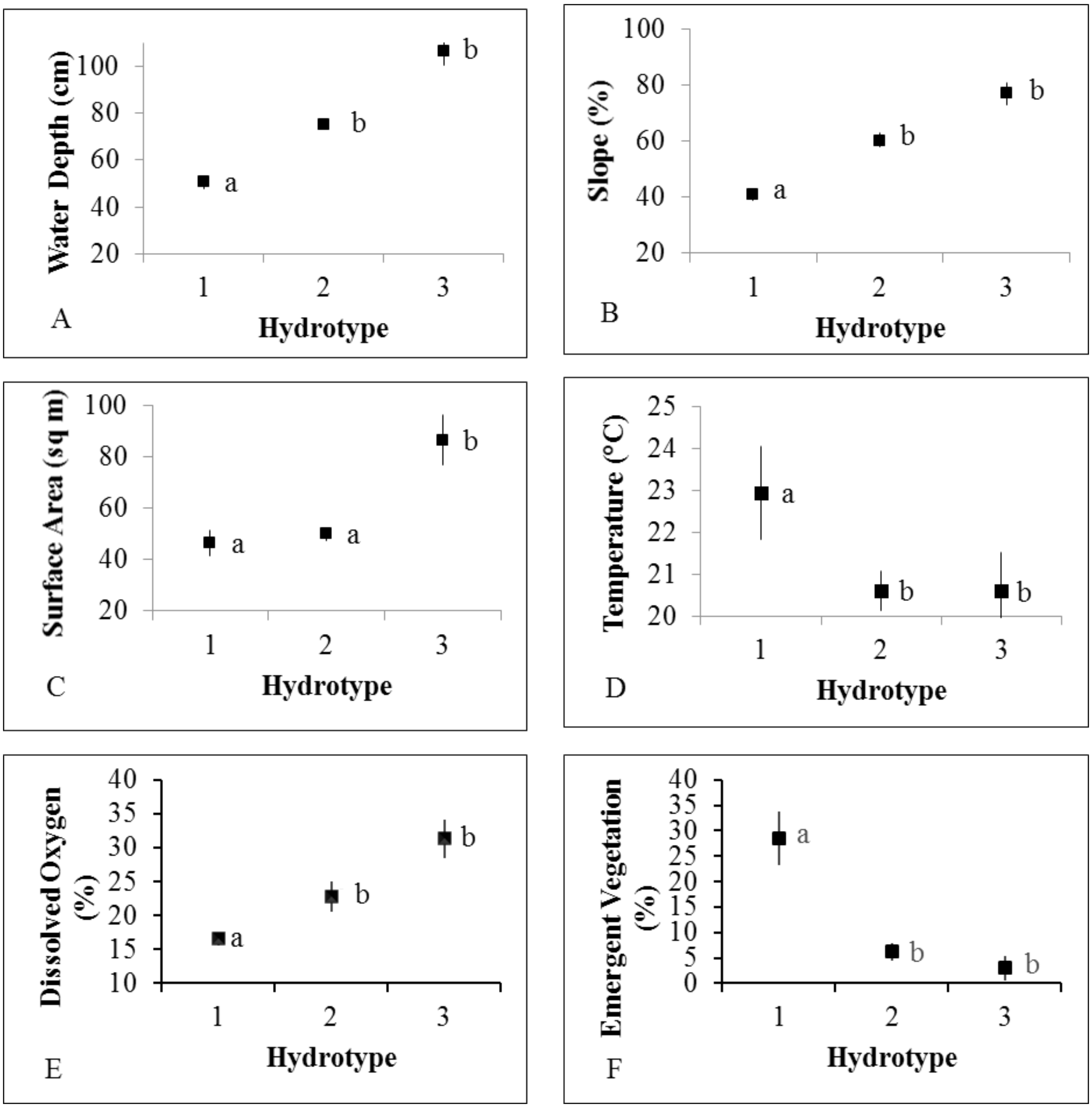

Figure 4. Mean (± SE) values of water depth (A), bank slope (B), pool size (C), water temperature (D), dissolved oxygen (E), and vegetative cover (F) among tank defilade hydrotypes 1 (temporary), 2 (semi-permanent), and 3 (permanent) in 2013. Letters a or b represent whether a variable was significantly different between hydrotypes. Results for 2012 are not depicted but have the same statistically supported patterns.

additional pools in 2012 only (10%), and six additional but different pools in 2013 only (13%), with a turnover of 28.2%. Cajun Chorus Frogs occurred in 28 pools (58%) both years, three pools in 2012 only (2%), and 10 additional but different pools in 2013 only (21%), with a turnover of 31.7%. Bronze Frogs occurred in one pool (2%) across both years, one pool in 2012 only (2%), and seven additional but different pools in 2013 only (15%), with a turnover of 89%. There was an overall decrease in occurrence of the less common species at our study site. Cricket Frogs used two pools across both years (4%), three in 2012 only (6%), and one additional but different pool in 2013 only (2%), with a turnover of 67%. Grey Tree Frogs (6%), Squirrel Tree Frogs (8%), and Eastern Narrow-Mouthed Toads (8%) were only confirmed in 2012. Fowlers Toads used one pool in 2013 only (2%). Green Sunfish (*Lepomis cyanellus*) and Mosquito Fish (*Gambusia affinis*) were the only common fish and were present in eight pools across both years of sampling. Four additional pools had fish present in 2012 but dried and we found four different pools with fish in 2013.

Discussion

The use of these tank defilades as an aquatic resource indicates that some historic military activity could have a positive effect on wildlife, particularly amphibians. Indeed, other studies have shown the beneficial impacts that ground disturbance and forest openings from military activity can have on native species, e.g., plants

Table 3. Parameter estimates from reverse stepwise regression models used to determine the best predictors of abundance (catch per unit effort in 2012 and 2013) for Cajun Chorus Frog (*Pseudacris fouquettei*; A, B), Southern Leopard Frog (*Lithobates sphenocephalus*; E, F), and presence-absence of Cajun Chorus Frogs (C, D) and Bronze Frogs (*Lithobates clamitans*; G) in 2013.

Species	Model	Parameter	Estimate	SE	Wald X^2	df	P
Cajun Chorus Frog	(A) 2012 Abundance	(Intercept)	−1.986	1.33	2.216	1	0.137
		Hydrotype (temporary)	2.356	0.93	6.389	1	0.011
		Fish (absence)	1.596	0.68	5.451	1	0.02
		Canopy closure	−0.020	0.01	4.822	1	0.028
	(B) 2013 Abundance	(Intercept)	−8.694	3.05	8.126	1	0.004
		Hydrotype (temporary)	3.079	0.65	22.494	1	< 0.001
		pH	1.158	0.46	6.293	1	0.012
	(C) 2012 Presence	(Intercept)	2.398	1.1	5.271	1	0.022
		Fish (absence)	4.007	1.14	12.44	1	< 0.001
	(D) 2013 Presence	(Intercept)	−0.336	0.59	0.33	1	0.566
		Fish (absence)	1.488	0.76	3.85	1	0.05
Southern Leopard Frog	(E) 2012 Abundance	(Intercept)	−1.420	0.75	3.594	1	0.058
		Hydrotype (temporary)	1.937	0.79	5.964	1	0.015
	(F) 2013 Abundance	(Intercept)	−0.330	1.19	0.077	1	0.781
		Hydrotype (temporary)	2.52	0.77	10.667	1	0.001
Bronze Frog	(G) 2013 Presence	(Intercept)	19.506	7.06	7.645	1	0.006
		Fish (absence)	5.763	2.32	6.153	1	0.013
		Slope of pool	21.322	8.16	6.823	1	0.009

(Leis et al. 2005), tortoises (Richter et al. 2011), and butterflies (Ferster and Vulinec 2010). Although created unintentionally, these tank defilade pools now serve as amphibian breeding habitat, and our results indicate that having pools with heterogeneous conditions (e.g., varying canopies, hydroperiods) benefit several species differently.

We found that pool characteristics, including hydroperiod, canopy closure, slope, pH, and fish affect amphibian presence and abundance. Hydrotype was a significant predictor across years for the three most abundant species; however, other variables explaining Cajun Chorus Frog abundance differed between study years. We are unable to explain the inter-annual differences in abundance, but a drought beginning in 2010 and lasting through 2011 may have contributed to lower Chorus Frog abundance in 2012. Pool hydroperiod was the primary variable affecting the distribution of species across pools, which is supported by analyses of the distribution and abundance of the two most common species and by comparison of community composition and similarity among hydrotypes. Wetland hydroperiod is a critical component of amphibian biology and can be a limiting variable because tadpoles must metamorphose before pools dry (Wellborn et al. 1996). Pools with permanent hydroperiods are often insufficient for certain species due to established predator populations and other features that are less suitable such as deep water and steep slopes (Calhoun et al. 2014; Kross and Richter 2016). Our results showed that Sorenson's and Jaccard's community similarity was lowest between the permanent hydrotype and those that dried, supporting previous studies (e.g., Drayer and Richter 2016). Sorenson's similarity index was higher than Jaccard's because it places more weight on species common to one hydrotype rather than species sharing two hydrotypes. Additionally, most pools with a permanent hydroperiod have established fish populations, which limit some groups of amphibian species from successfully breeding in them such as Chorus Frogs and Grey Tree Frogs. Conversely, other groups (e.g., Cricket Frogs, Bronze Frogs) require permanent water for multi-seasonal larval stages (Shulse et al. 2010). Therefore, different amphibian communities often inhabit pools across the hydroperiod gradient (Wellborn et al. 1996; Drayer and Richter 2016). We only found Bronze Frogs in semi-permanent and permanent pools. The hydrotype of tank defilades contributed to predicting the abundance of Cajun Chorus Frogs, Southern Leopard Frogs, and presence of Bronze Frogs. We found Chorus Frogs and Southern Leopard Frogs in temporary to semi-permanent pools, which corroborates previous studies

Table 4. Larval amphibian species richness and diversity index for each wetland hydrotype and similarity indices for each pair of hydrotypes. Wetland permanence categories are based on the number of months tank defilades held water (see text). Scale of similarity ranges from 0.00 (low) to 1.00 (high).

Hydrotype/Comparison	Species Richness	Shannon-Wiener Index	Jaccard's Coefficient	Sorenson's Coefficient
Temporary	6	1.43	—	—
v. Semi-permanent	—	—	0.86	0.92
v. Permanent	—	—	0.50	0.67
Semi-permanent	7	1.64	—	—
v. Permanent	—	—	0.63	0.77
Permanent	6	1.61	—	—

of other species: abundance is often inversely related to aquatic permanency (Kolozsvary and Swihart 1999; Werner et al. 2009; Shulse et al. 2010).

We confirmed Cajun Chorus Frog larvae in 26 fishless temporary/semi-permanent pools. This is consistent with their life history and other studies of chorus frogs (*Pseudacris* sp.) that also found a negative association with fish presence (Hecnar and M'Closkey 1997; Porej and Hetherington 2005; Shulse et al. 2012). Conversely, Bronze Frog presence was positively associated with steeper slopes, which supports results of Shulse et al. (2010) in northern Missouri that included a positive correlation between within-wetland slope and Green Frog (*Lithobates clamitans*) abundance. Slope, water depth, and temperature were different among pool hydrotypes, whereby pools with short hydroperiod had a more gradual slope, shallower depths, smaller average wetted surface area, lower temperature, and the absence of established fish populations compared to pools with longer hydroperiods. Therefore, it is difficult to separate the individual effects of these pool characteristics from the effect of hydroperiod, although they can each be important for amphibians. Gradual slope and shallow water provide habitat for calling, thermoregulation, foraging, and refuge from predators (Semlitsch 2002; Calhoun et al. 2014). Although no one has explicitly tested a series of slopes to determine the best for breeding amphibians, other studies have documented the importance of gradual slopes for Boreal Chorus Frogs (*Pseudacris maculata*), Western Chorus Frogs (*Pseudacris triseriata*), Northern Leopard Frogs (*Lithobates pipiens*), and Gray Tree Frogs (*Hyla versicolor*; Porej and Hetherington 2005; Shulse et al. 2012).

Cajun Chorus Frogs were negatively associated with canopy closure. This is consistent with *Pseudacris* sp. life history and prior studies showing closed canopies can affect amphibian population size (Burne and Griffin 2005; Skelly et al. 2005; Thurgate and Pechmann 2007; Werner et al. 2009) and were often sink habitats for Chorus Frogs (*Pseudacris triseriata*) (Werner et al. 2009). Canopy also varied independently of hydrotype, supporting its importance to breeding amphibians. Canopy can affect water chemistry (i.e., pH, dissolved oxygen), temperature, and primary productivity (plant abundance), which have been documented to affect species composition (Calhoun et al. 2014). Cajun Chorus Frog reproduction often begins as early as October when temperatures are between 4 to 21° C (Lemmon et al. 2007), explaining the inclination toward pools with more sun exposure.

Surprisingly, emergent vegetation was not a significant factor for species abundance at our study site, although other studies have shown amphibian preference for wetlands with aquatic vegetation. In Missouri, Shulse et al. (2010) found that Boreal Chorus Frogs were most abundant in heavily vegetated wetlands, and Burne and Griffin (2005) associated richness of amphibian species to percentage of emergent vegetation. The amount of vegetation at our study site was relatively low and consistent across the pools. Additionally, each pool had a high abundance of pine needles on the pool basin that may have provided sufficient cover for larvae and structure for attaching egg masses.

Our results highlight the importance of protecting mosaics of small man-made pools for conservation of amphibians and other wildlife. Although no species of conservation concern were observed during our study, the habitat should be considered important because it is being used for breeding by multiple common frog species and were visited by multiple reptile species including turtles, snakes, and American Alligators (*Alligator mississippiensis*). At-risk species potentially occurring in the region, such as the Crawfish Frog (*Lithobates areolatus*), would likely use habitat similar to the mosaic described in our study. Current Army policy requires that any disturbances from training, historic or current, need to be repaired or filled in after training is completed. However, this study demonstrates that the Army created an ecologically valuable habitat (i.e., tank defilades), and we suggest that some disturbances from military training, particularly historical, could be beneficial. Existing pools that hold water for various durations of time are being used by a variety of species and should be protected and monitored when possible. Conservation planning for pool-breeding amphibians should be informed from habitat investigations at multiple scales (Baldwin et al. 2006; Marsh and Trenham 2001; Semlitsch 2002; Porej et al. 2004). Characteristics of these unintentionally developed pools have provided us with insight into what makes functionally suitable breeding habitat for three amphibian species, supporting the need for continued research and monitoring on the function of these pools. Wetlands constructed for mitigation or conservation should be built with consideration for function and quality, not quantity exclusively (Semlitsch 2008; Calhoun et al. 2014). Our study and additional research may provide local land managers with valuable information to protect and create suitable breeding habitat that requires using a limited portion of available training lands.

We recommend that temporary hydrology, gradual slopes, shallow depths, and varying levels of canopy closure be considered in any future aquatic resource development plans. Our study sites are congregated close together on the same landscape allowing us to study amphibian breeding habitat at the pool-scale. Landscape-scale habitat characteristics were not analyzed as part of this study. However, in addition to the pool characteristics mentioned above, we suggest that the Army and U.S. Forest Service consider landscape level perspectives, recommended in the literature, if more pools are constructed. Land managers should identify clay-based soils that will drain relatively slowly compared to the common sandy soils of the Long-leaf Pine ecosystem (Biebighauser 2011; Calhoun et al. 2014). If pools need to be created in areas without clay soils, the basin must be constructed to be lower than the water table for a portion of the year, but this might require hydrologic studies to determine monthly trends in water table level (Biebighauser 2011). As previous studies have recommended (Semlitsch 1998), land managers should consider areas with surrounding intact forests that will support all stages of the amphibian life cycle with few paved roads and low expected training activity. We also suggest creating pools well dispersed across the landscape while allowing for breeding habitat connectivity (Burne and Griffin 2005).

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Appendix I. Matrix of ranked correlation coefficients (Spearman's r) among the environmental variables sampled in 48 pools. For variables measured multiple times per year (number reported in parentheses) mean values were correlated. Correlations for 2012 are on the left of the diagonal and for 2013 are to the right of the diagonal. Significant correlations ($P < 0.05$) are indicated with an asterisk. Variables that were not highly correlated with each other (< 0.70) were included in linear regression modeling. Variables that were excluded because of r > 0.70 with another variable are shown in **bold**. We removed water temperature because we wanted to focus on variables directly related to pool morphology and removed center depth because it was correlated with both slope and surface area. Variable abbreviations are CC = Canopy Closure, Veg = Vegetation, WSA = Wet Surface Area, CD = Center Depth, WT = Water Temperature, DO% = Percentage of Dissolved Oxygen, and Cond = Conductivity.

2012/2013 (number of times sampled/year)	CC	Veg	Slope	WSA	CD	WT	pH	DO%	Cond
Canopy Closure (1/0)	1	−0.41*	0.05	−0.34*	0.08	0.17	−0.37*	−0.33*	0.15
Vegetation (1/1)	−0.31*	1	−0.57*	−0.16	−0.56*	−0.68*	−0.14	−0.14	0.09
Slope (6/7)	−0.06	−0.41*	1	0.27	**0.81***	**0.81***	0.35*	0.51*	−0.34*
Wet Surface Area (6/7)	−0.42*	−0.18	0.50*	1	0.58*	0.28	0.15	0.60*	−0.37*
Center Depth (6/7)	−0.11	−0.42*	**0.91***	**0.71***	1	**0.73***	0.24	0.69*	−0.34*
Water Temperature (6/7)	0.04	−0.27	0.13	0.00	0.09	1	0.27	0.43*	−0.17
pH (6/7)	−0.24	−0.19	0.34*	0.38*	0.35*	0.24	1	0.33*	0.19
DO% (6/7)	−0.38*	−0.25	0.58*	0.64*	0.62*	0.39*	0.51*	1	−0.41*
Conductivity (6/7)	0.06	0.08	0.03	−0.01	−0.03	0.07	0.23	−0.15	1

Appendix II. Seven reptile species observed using the tank defilade pools.

Species		Years Observed
Common Snapping Turtle	*Chelydra serpentina*	2012–2013
Red-Eared Slider	*Trachemys scripta*	2012–2013
Mississippi Mud Turtle	*Kinosternon subrubrum*	2012–2013
Yellow-Bellied Watersnake	*Nerodia erythrogaster*	2012–2013
Cottonmouth Snake	*Agkistrodon piscivorus*	2012–2013
Western Ribbon Snake	*Thamnophis proximus*	2012–2013
American Alligator	*Alligator mississippiensis*	2012