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Management and Conservation

Amphibian Communities in Natural and Constructed Ridge Top Wetlands With Implications for Wetland Construction

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ABSTRACT Among the many causes linked to amphibian declines, habitat loss and alteration remain the most significant. Lack of federal protection for isolated wetlands has resulted in loss of amphibian breeding habitat without subsequent mitigation. Additionally, wetlands built for mitigation often do not replicate lost natural wetlands in structure or ecological processes. The long-term role of constructed wetlands for amphibian conservation is poorly understood because monitoring is often lacking. Our objective was to compare amphibian communities of natural wetlands to 2 types of constructed wetlands in the Daniel Boone National Forest, Kentucky. We measured habitat variables including canopy closure, hydrology, upland coarse woody debris, aquatic vegetation, maximum water depth, and Ohio Wetland Rapid Assessment Score at each wetland and quantified species-specific amphibian capture per unit effort using dip-netting. Wood frogs (*Lithobates sylvaticus*) and marbled salamanders (*Ambystoma opacum*) were almost exclusively found in natural, ephemeral wetlands, whereas large frogs (*L. clamitans*, *L. catesbeianus*, *L. palustris*) were primarily found breeding in permanent, constructed wetlands. Permutational analysis of variance indicated significant differences in amphibian communities between constructed and natural wetland types. Redundancy analysis indicated that hydrology and canopy closure best explained the differences in community composition between natural and constructed wetlands. Regression analyses and subsequent model ranking showed that greater captures per unit effort for eastern newts (*Notopthalmus viridescens*) and green frogs (*L. clamitans*) were predicted by increasing wetland size and depth, respectively, whereas mole salamanders (*Ambystoma* sp.) were negatively associated with the amount of aquatic vegetation and positively associated with wetland depth. As amphibian conservation and management become increasingly important in light of recent population declines and habitat loss, the ability to construct wetlands that provide amphibian habitat and to monitor how amphibians respond will be crucial to preservation of species diversity. Our research underscores the need for monitoring constructed wetlands to assess ecological condition. We provide suggestions to land managers who aim to construct isolated wetlands for amphibians.

KEY WORDS amphibians, constructed wetlands, Kentucky, *Lithobates catesbieanus*, *Lithobates sylvaticus*, *Notophthalmus viridescens*, wetlands.

Most amphibians have a biphasic life history and depend on the quantity, quality, and spatial configuration of both terrestrial and aquatic environments. Even amphibians without an aquatic egg stage require moisture to reproduce. In forested habitats, this source of water is most often from streams or isolated wetlands (Wells 2007). Hydrologically isolated wetlands are priorities for conservation because of annual variability in hydroperiod and sensitivity to disturbance (Semlitsch and Bodie 1998). Isolated wetlands can function as stepping-stone connections among amphibian populations and breeding habitat for endemic species (Zedler 2003, Egan and Paton 2004). Many amphibians have greater reproductive success in isolated wetlands and other temporary bodies of water because they lack fish predators (Wellborn et al. 1996), and amphibian biomass at these sites can be high (Calhoun et al. 2003, Gibbons et al. 2006).

Similar to other areas throughout the United States, Kentucky has lost the majority (>81%) of its historical natural wetlands (Dahl 2000). The remaining 1,214 km^2 of Kentucky wetlands are mostly palustrine, forested wetlands characterized by hydrophytic trees, shrubs, and herbaceous plant species (Environmental Law Institute 2007). Among these, ridge top vernal wetlands have long been described as unique habitats (Braun 1937). These small, isolated wetlands are common to the Cumberland Plateau, and have relatively high amphibian species richness (Corser 2008). Despite vernal wetlands being part of the forested landscape and significant to biodiversity conservation, federal

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protection laws are lacking, and only 6 states (Indiana, Ohio, Tennessee, Virginia, Washington, and Wisconsin) explicitly regulate activities in hydrologically isolated wetlands.

Although a goal of wetland mitigation is to replace lost wetland functionality, wetlands constructed through mitigation often fail to duplicate natural processes (Lichko and Calhoun 2003, Moreno-Mateos et al. 2012). Additionally, mitigation projects often exhibit a lack of monitoring, poor record keeping, and lack of consistency in implementation (D'Avanzo 1990, Turner et al. 2001, Lichko and Calhoun 2003, Minkin and Ladd 2003, Mack and Micacchion 2006, reviewed in Kihslinger 2008). Constructed wetlands often vary widely in terms of hydroperiod (i.e., the length of time surface water is present; Gamble and Mitsch 2008). Hydrology affects amphibian community composition, with numerous species only found in ephemeral wetlands that typically dry at least once annually (hereafter referred to as ephemeral wetlands; Snodgrass et al. 2000). In 2008, the United States Army Corps of Engineers issued revised regulations to unify the requirements of mitigation and to provide more organization for monitoring and record-keeping (Environmental Protection Agency 2008), but these regulations do not address the need for improved construction methods.

Constructed wetlands created for game wildlife habitat enhancement also provide habitat for amphibians (Pechmann et al. 2001, Knutson et al. 2004, Balcombe et al. 2005, Porej and Hetherington 2005, Vasconcelos and Calhoun 2006). Although constructed wetlands provide amphibian breeding habitat and have been partially successful in mitigating lost habitat in Carolina Bay ecosystems, amphibian communities may not be similar to those found in lost wetlands (Pechmann et al. 2001). Additionally, constructed wetlands might act as ecological sinks where larval survival is reduced (DiMauro and Hunter 2002) or become areas of low amphibian diversity (Porej and Hetherington 2005). Although previous studies were instrumental in documenting use of constructed wetlands by amphibians, most lacked reference wetlands for comparison (Babbitt and Tanner 2000, Petranka et al. 2003, Porej and Hetherington 2005, Vasconcelos and Calhoun 2006, Shulse et al. 2010) or focused on wetlands that were not intentionally constructed for wildlife (Lehtinen and Galatowitsch 2001, DiMauro and Hunter 2002, Hazell et al. 2004, Knutson et al. 2004).

More than 400 wetlands have been constructed over the past 22 years within the Daniel Boone National Forest (DBNF) in Kentucky for habitat enhancement, game use, and Indiana bat (*Myotis sodalis*) conservation, but few have been monitored after construction (T. R. Biebighauser, U.S. Forest Service, personal communication). Although these wetlands were not originally constructed for mitigation or amphibian management, documenting differences in amphibian communities and habitat between constructed and naturally occurring wetland types will assist land managers in constructing wetlands with desirable characteristics for amphibians. Additionally, understanding how vegetation, hydrology, and other local wetland features affect individual amphibian species will improve our ability to incorporate these features into future wetland construction. Our objective was to determine if amphibian communities differed between natural wetlands and wetlands constructed using different methods in the DBNF. Specifically, the following questions were addressed: 1) How do natural wetlands differ from wetlands of different construction types in amphibian community composition and 2) What habitat variables associated with constructed and natural wetlands predict the presence and capture per unit effort (CPUE) of individual amphibian species?

STUDY AREA

Study sites were located within the DBNF, eastern Kentucky (Table 1). Our study focused on the Cumberland District, the northernmost district of the DBNF. Surveyed wetlands were located in Bath and Menifee Counties. The majority of the wetlands constructed in the DBNF are isolated, on ridge tops, fishless, and surrounded by deciduous forests. Density of constructed wetlands within the Cumberland District and the consistency with which they have been built provides an opportunity for monitoring many wetlands across multiple construction classes within the same physiographic region, the Western Allegheny Plateau (Woods et al. 2002).

We selected wetlands for this study by ground-truthing 38 wetlands that were mapped in a geographic information system (GIS). We categorized wetlands by construction method and randomly selected study sites from each group. We determined sample sizes by estimating the number of wetlands that we could survey for amphibians within a 24-hour period. We categorized constructed wetlands into new construction method (built 2004–2007; $n = 7$) and old construction method (built 1988–2003; $n = 7$). From 1988 to 2003, wetlands were constructed with dams to hold water permanently. Since 2003, construction protocols were adjusted to provide smaller, shallower wetlands with increased amounts of upland coarse woody debris (CWD) to replicate conditions associated with natural, ephemeral ridge top wetlands of the region. One wetland, Kidney88, was the exception (Table 1). This wetland was built in 1988, but exhibited characteristics more indicative of the newer construction method; therefore, we classified it as newer construction. We designated all known natural wetlands located in the study area as the third study group ($n = 5$).

Based on weather data for 1970–2010 collected by the National Oceanic and Atmospheric Administration at a weather station approximately 8 km from our study area (ID: Farmers 2S, Rowan County, Kentucky), mean monthly temperature from May to August of 2010 ($\bar{x} = 22.1°$ C, SE = 2.0) was comparable to the average temperature for 1970–2009 ($\bar{x} = 20.0°$ C, SE = 2.2). Mean monthly precipitation for our study ($\bar{x} = 5.4$ cm, SE = 1.9) was also comparable to average precipitation between 1970 and 2009 ($\bar{x} = 4.6$ cm, SE = 0.3).

METHODS

We sampled amphibians using a standardized dip-netting protocol (Shaffer et al. 1994) in which we took dip-net

Table 1. Characteristics of the 19 wetlands surveyed for amphibians in the Daniel Boone National Forest, Kentucky, May–August 2010.

Name	Year constructed	Wetland type	Distance to nearest wetland (m)[a]	Dip net sweeps[b]	Size (m^2)
60/70s	ca. 1970	Old method	634	9.4 (0.15)	90
040–90	1990	Old method	637	11.0 (0.00)	141
09rework	1992	Old method	637	8.0 (0.00)	115
42–93	1993	Old method	597	13.0 (0.00)	127
95NEW	1995	Old method	708	9.4 (0.15)	160
060–96	1996	Old method	413	14.2 (0.12)	236
35–97	1997	Old method	295	11.4 (0.16)	113
Kidney88	1988	New method	530	5.8 (0.12)	35
04A	2004	New method	919	5.8 (0.12)	35
05A	2005	New method	919	5.0 (0.00)	38
06A	2006	New method	119	9.2 (0.12)	71
06C	2006	New method	119	2.8 (0.12)	16
06D	2006	New method	146	6.6 (0.15)	113
06E	2006	New method	146	6.0 (0.00)	44
DC2		Natural	415	17.5 (0.16)	441
DC5		Natural	275	10.2 (0.12)	99
DC6		Natural	275	10.0 (0.00)	207
DC0		Natural	322	12.4 (0.16)	91
Booth		Natural	145	20.8 (0.12)	613

[a] Distance to nearest wetland was measured by calculating distance between wetland centers.
[b] Average (standard error) number of dip net sweeps per 1-day survey.

samples every 5 m while walking the wetland edge. A sample consisted of guiding the d-frame net in a 180° arc from the shoreline while repeatedly jabbing the net into the substrate. We surveyed each study wetland during a single sampling period per month, May–August 2010. We chose survey dates to maximize detectability for the amphibian species of the region (Dodd 2004). In each sampling period, we surveyed a wetland for amphibians on 3 consecutive days. Because of logistics and travel distance between wetlands, we split wetlands into 2 groups; we surveyed each group during separate, consecutive 3-day spans.

During the initial 2 months of the study, we evaluated the potential for recaptures by clipping the tails of captured larvae. After 2 sample periods of no recaptures, we assumed that resampling the same larvae across months was unlikely. To prevent counting individual larva multiple times within a monthly sample period, we selected 1 sample event per species per month based on the day with the greatest abundance for each species. We then totaled this value for the 4 sampling periods to index the abundance (measured as CPUE) of each species for the breeding season. We released all amphibians captured immediately after being identified to species and life stage (Dodd 2004). Individuals used for statistical analyses were larvae with the exception of eastern newts (*Notopthalmus viridescens*), which were adults. Eastern newts have a complex life cycle that includes an adult, aquatic breeding phase. We interpreted CPUE of these adults as a measure of breeding output within the wetland. Our sampling and animal handling protocols were approved by Eastern Kentucky University's Institutional Animal Care and Use Committee (protocol # 08-2010).

We calculated CPUE for each species during every sampling event (number of individuals captured/number of dip-net sweeps at each wetland; Shono 2008, Shulse et al. 2010). We used the greatest CPUE value for each species during each sampling period and summed them across the 4 months. To test for a potential confounding effect of wetland age in explaining species CPUE, we performed Pearson correlations between species-specific CPUE and wetland age. We assumed that a non-significant relationship between CPUE and wetland age indicated that age was not confounding construction technique in our analyses.

At each wetland, we measured characteristics that are typically associated with amphibian habitats. For this study, we defined wetland hydrology as either ephemeral or permanent. We surveyed aquatic vegetation using a 1-m^2 quadrat placed on the edge of the wetland at each of the cardinal directions and at the center of the wetland. We visually estimated the total percentage of vegetation cover within the quadrat and averaged totals across the 5 samples. We estimated percent overstory canopy closure directly above each aquatic vegetation quadrat with a spherical densiometer (Jennings et al. 1999) and averaged percentages across the 5 sample points. We recorded wetland depth at the deepest point of each wetland during each sampling period. We scored each site for wetland quality according to the Ohio Rapid Wetland Assessment Method (ORAM), a metric-based assessment for ecological quality and level of function for a particular wetland (Mack 2001). For full description of ORAM, see Mack (2001); briefly, it is composed of metrics to assess wetland condition, including hydrology (duration of inundation, depth, and modifications of natural hydrologic regime), habitat alteration, plant community diversity, interspersion, and microtopography (i.e., habitat complexity). We measured upland CWD according to a line-intersect sampling protocol from Waddell (2002) in which 50-m transects were positioned and oriented in each cardinal direction perpendicular to the wetland border (Warren and Olsen 1964). For upland CWD with a diameter $\geq$10 cm at its narrowest end that intercepted each transect, we measured total length and diameter at the narrowest and widest ends (DiMauro and Hunter 2002, Waddell 2002). We used these measurements to calculate cubic volume of CWD per hectare (Husch et al. 1972, Waddell 2002 after DeVries 1973). We compared each habitat variable between groups using a 1-way analysis of variance (ANOVA) with a Tukey post hoc comparison test. If the assumption of equal variance was not met, we used a Welch's ANOVA with a Tukey post hoc comparison test. As above for CPUE, we identified potential confounding effects of wetland age on habitat variables using Pearson correlations between each habitat measurement and wetland age, regardless of wetland type. We assumed that a non-significant association between habitat variables and wetland age indicated that age was not confounding construction technique in our analyses.

We examined amphibian community data and all habitat variables for constructed and natural wetlands using redundancy analysis (RDA) in R Version 2.12.1 (R Development Core Team, Vienna, Austria) with package VEGAN (Oksanen et al. 2011). We used a Hellinger transformation of species data to meet normality assumptions (Legendre and Gallagher 2001). We used permutation tests using the anova.cca command in Program R to examine significance of individual habitat parameters and axes used in RDA plots (Oksanen 2011). To test for differences in amphibian community composition between the construction types and natural wetlands, we conducted a permutational multivariate analysis of variance using a distance matrix (ADONIS) in R. We selected the Bray-Curtis Similarity Index as the distance measure based on its success in approximating ecological distance (Bray and Curtis 1957, Faith et al. 1987) using 10,000 permutations. We adjusted alpha for pairwise comparisons between the 3 groups by calculating sequential Bonferroni corrected P values (Rice 1989). In addition to the RDA procedure, we calculated Shannon-Wiener Index values for each wetland group to provide an estimate of species diversity.

Different amphibian species vary in response to the same suite of habitat variables, and null hypothesis testing may be inappropriate for ecological studies with many predictor variables (Anderson et al. 2000, Gardner et al. 2007). Thus, we analyzed species separately using a model selection (information-theoretic) approach with amphibian CPUE as the response variable and the habitat parameters as predictor covariates. Using generalized linear modeling in SPPS version 17.0 (SPSS, Inc., Chicago, IL), we evaluated 12 regression models with a compound Poisson (Tweedie) distribution and log-link function (Shono 2008, Shulse et al. 2010; Table 2). We chose the Tweedie distribution because it can accommodate discrete and continuous data, large numbers of zeroes, and because count data are continuous when converted to CPUE. The index parameter value (P), which is the parameter in the model that varies depending on data continuity, can range between 1 and 2 for CPUE data. The index parameter determines the shape of the probability distribution (Shono 2008). We used Pearson chi-square for estimating the parameter value in our models to obtain more conservative variance estimates as recommended by McCullagh and Nelder (1989). We evaluated models for species with a sufficient CPUE to allow statistical analysis. First, we assessed the global model for fit by examining a plot of residuals against the predicted values. If the global model fit the data, we calculated Akaike's Information Criterion values corrected for small sample sizes (AIC_c) and ranked the models (ΔAIC_c; Burnham and Anderson 2002). We reported all models with a $\Delta AIC_c \leq 2.0$. If multiple candidate models had $\Delta AIC_c \leq 2.0$, we used model averaging across all candidate models to investigate the relative importance of each parameter within the top models and calculated 85% confidence intervals to make confidence intervals AIC compatible as recommended by Arnold (2010).

Table 2. Candidate models for predicting amphibian capture per unit effort in ridge top wetlands, Daniel Boone National Forest, Kentucky, May–August 2010.

Model variables[a]	Model type[b]
Wetland type, size, canopy closure, CWD, depth, ORAM, vegetation	Global
Wetland type, ORAM	Quality measurement
Depth, size, wetland type	Construction variables
Wetland type	Wetland type
Wetland type, size, canopy closure, depth	Construction including tree removal
Wetland type, depth	Construction based on depth
ORAM	ORAM
Canopy closure, CWD	Outside-wetland
Canopy closure	Forest management
Size	Wetland size
Vegetation	Vegetation
Depth, vegetation, size	Within-wetland

[a] Wetland type = natural, old method construction, or new method construction; CWD = upland coarse woody debris; ORAM = Ohio Rapid Wetland Assessment Method score; vegetation = percent cover of aquatic vegetation.

[b] Variable combinations represent different environmental or wetland construction strategies.

RESULTS

Habitat and Amphibian Community Comparisons

We found no correlation between wetland age and CPUE for any amphibian species (all $P \geq 0.215$) or any measured habitat variable (all $P \geq 0.192$); hence, we determined that wetland age was not confounding construction technique. Additionally, Pearson correlations revealed that ORAM score was associated with canopy closure ($r = 0.63$, $P = 0.004$) and wetland size ($r = 0.789$, $P < 0.001$). Although ORAM score was correlated with canopy closure and wetland size, we included all the variables in the RDA because ORAM represented multiple habitat variables and we wanted to evaluate its utility for monitoring wetland quality (Mack 2001). Hence, caution should be used in interpreting the influence of ORAM score within the RDA analysis because of a potential inflation of importance.

All natural wetlands dried during the summer of 2010 (2 in Jun, 1 in Aug, and 2 in Sep). Two of the new construction method wetlands dried in June and July, respectively. Water persisted in all old construction method wetlands throughout the summer. Post-hoc Tukey multiple comparison tests revealed that old construction method wetlands were deeper than new construction method ($P = 0.003$, mean difference = 55.4 cm ± 13.7 SE) and natural ($P = 0.002$, mean difference = 62.5 cm ± 15.0 SE) wetlands. Natural wetlands had greater average ORAM scores than both types of constructed wetlands ($F_2 = 34.77$, $P < 0.001$). Natural wetlands also scored higher in 3 metrics of the ORAM: hydrology, habitat alteration and development, and the plant communities, interspersion, and microtopography metrics (Fig. 1). Overstory canopy closure was greater at natural wetlands compared to constructed wetlands (Welch's ANOVA, $P = 0.048$ and mean difference = 25.4% ± 9.9 SE for new construction, $P = 0.052$ and mean difference = 26.8% ± 9.9 SE for old construction methods). The amount of upland CWD surrounding wetlands and the percent of aquatic vegetation did not differ among wetland types (CWD: $F_2 = 2.42$, $P = 0.121$; vegetation: $F_2 = 0.411$, $P = 0.670$).

We captured 4,218 individuals representing 13 species (Table 3); county records indicate that the only wetland-breeding species known to occur in the area that were not detected included eastern spadefoot toad (*Scaphiopus holbrookii*) and mountain chorus frog (*Pseudacris brachyphona*; John MacGregor, Kentucky Department of Fish and Wildlife Resources, personal communication). After choosing the sampling events with the greatest number of captures per species from each month, we used 2,372 captures for statistical analyses. We captured the most individuals in natural wetlands (1,315) compared to the new construction method (407) and old construction method (650) wetlands. Natural wetlands had the greatest total species richness (12) compared to the new construction method (10) and old construction method (10) wetlands. However, all wetland types had similar mean Shannon-Wiener Diversity Index scores (natural: 0.91 ± 0.33 SE, new construction method: 1.06 ± 0.19 SE, old construction method: 1.39 ± 0.14 SE), indicating that species richness and evenness did not differ. We detected multiple species at all wetlands, except for a single new construction method wetland where we only captured eastern newts.

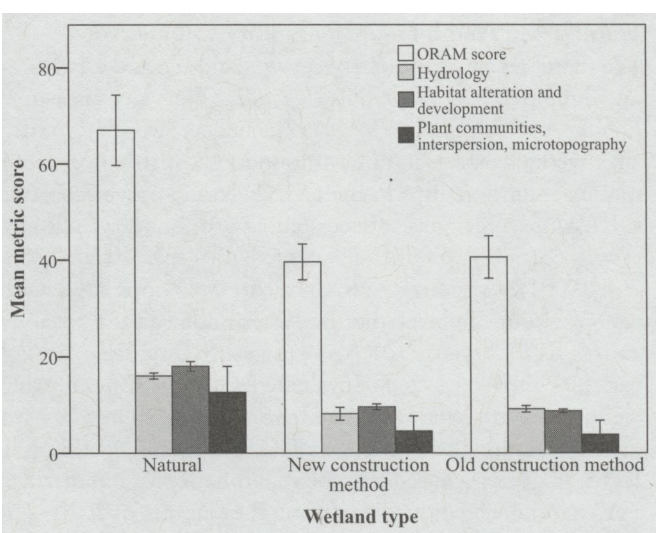

Figure 1. Three mean metric scores (hydrology; habitat alteration and development; plant communities, interspersion, and microtopography) and total Ohio Rapid Assessment Method (ORAM) score for 3 wetland types within the Daniel Boone National Forest, Kentucky, May–August 2010.

Prior to the RDA, we log transformed the variable upland CWD because of extreme outliers in the raw data that we detected by examining boxplots. We removed 1 site within the new construction method group (06C; Table 1) from the RDA analysis because we did not capture any individuals at the site. The RDA accounted for 52% of the total variation in CPUE and habitat data, and the ordination result was significantly different from random ($F_6 = 2.01$, $P = 0.008$; Fig. 2). The RDA1 and the RDA2 axes accounted for 66.5% and 17.3% of the explained variation, respectively. Hydrology and amount of canopy cover were significant vector terms (hydrology: $F_1 = 5.35$, $P = 0.003$; canopy cover: $F_1 = 2.32$, $P = 0.044$). Using the ADONIS procedure, we found significant differences between wetland types in amphibian community composition (global $R_2 = 0.257$, $P = 0.008$), in which natural wetlands were significantly different from old construction method wetlands ($F_1 = 4.85$, $P = 0.006$). New construction method wetlands were not significantly different from old construction method wetlands ($F_1 = 0.79$, $P = 1.00$) or natural wetlands ($F_1 = 2.44$, $P = 0.074$).

Individual Species Associations

We evaluated Tweedie regression models for 5 species (see Table S1, available online at www.onlinelibrary.wiley.com). We combined 2 species, spotted and Jefferson salamander (*Ambystoma maculatum* and *Am. jeffersonianum*), based on similar life histories (Shulse et al. 2010). For each of these model evaluations, 2–3 models were closely ranked; therefore, we were unable to declare a single best model (Table 4). We used model averaging to produce parameter estimates of these top ranking models for each species (Table 5).

Green frogs (*Lithobates clamitans*) and American bullfrogs (*L. catesbeianus*) were the most commonly detected anuran species (Table 3). Except for <5 larvae of both species found in a single natural wetland, we detected all green frog and American bullfrog larvae in constructed wetlands. The natural wetland with green frog and American bullfrog larvae was approximately 100 m from a permanent wetland and dried in September. Green frog CPUE was best predicted by models that included wetland type, maximum depth, and wetland size (Table 4). Model averaging of individual parameters showed that green frogs were negatively associated with natural wetlands and positively associated with wetland depth (Table 5). Cope's gray treefrog (*Hyla chrysoscelis*) CPUE was best predicted by models that included size, wetland type, and depth (Table 4). However, these predictors had confidence intervals that overlapped zero (Table 5). Spring peepers (*P. crucifer*) were positively associated with wetland size and negatively associated with depth and natural wetlands (Table 5). Spotted and Jefferson salamander larvae were the most widespread caudate species and were found in all wetland types. The top-ranked models for

Table 3. Amphibian species captured during surveys of constructed and natural wetlands in the Daniel Boone National Forest, Kentucky, May–August 2010. NC = not captured in this wetland type. CPUE = capture per unit effort.

			Mean CPUE ± SE			Detection probability (*P*)	
Scientific name	**No. individuals**	**% of wetlands present**	**Natural**	**Old construction method**	**New construction method**	**Best model**	**Detection probability**
Anaxyrus americanus (American toad)	175	10.5	0.76 ± 0.68	NC	3.55 ± 3.55	Survey-specific *P*	0.00–1.00
An. fowleri (Fowler's toad)	25	10.5	0.33 ± 0.29	NC	0.05 ± 0.05	Constant *P*	0.01
Hyla chrysoscelis (Cope's gray treefrog)	123	42.1	0.70 ± 0.63	0.17 ± 0.10	0.81 ± 0.49	Survey-specific *P*	0.00–0.75
Pseudacris crucifer (spring peeper)	95	31.6	0.64 ± 0.57	0.25 ± 0.16	0.39 ± 0.37	Survey-specific *P*	0.00–0.83
Lithobates sylvaticus (wood frog)	993	21.1	18.82 ± 7.81	NC	NC	Survey-specific *P*	0.00–1.00
L. clamitans (green frog)	169	57.9	0.01 ± 0.01	1.68 ± 0.89	0.99 ± 0.56	Constant *P*	0.35
L. catesbeianus (American bullfrog)	65	47.4	0.03 ± 0.03	0.56 ± 0.23	0.54 ± 0.28	Survey-specific *P*	0.00–0.77
L. palustris (Pickerel frog)	7	10.5	NC	0.10 ± 0.08	NC	Constant *P*	0.09
Hemidactylium scutatum (four-toed salamander)	11	31.6	0.05 ± 0.03	0.03 ± 0.02	0.02 ± 0.02	Constant *P*	0.04
Ambystoma opacum (marbled salamander)	26	21.1	0.59 ± 0.40	0.03 ± 0.03	NC	Survey-specific *P*	0.00–1.00
Am. maculatum (spotted salamander)	327	84.2	0.70 ± 0.29	2.70 ± 0.83	1.51 ± 0.76	Survey-specific *P*	0.19–0.81
Am. jeffersonianum (Jefferson salamander)	93	78.9	0.18 ± 0.11	0.86 ± 0.25	0.24 ± 0.17	Survey-specific *P*	0.00–0.76
Notopthalmus viridescens (eastern newt)	263	73.7	0.07 ± 0.04	1.95 ± 0.55	1.70 ± 0.69	Survey-specific *P*	0.08–0.92

the combined *Ambystoma* included total aquatic vegetation, maximum depth, and approximate wetland size (Table 4). The combined *Ambystoma* were negatively associated with aquatic vegetation and positively associated with depth

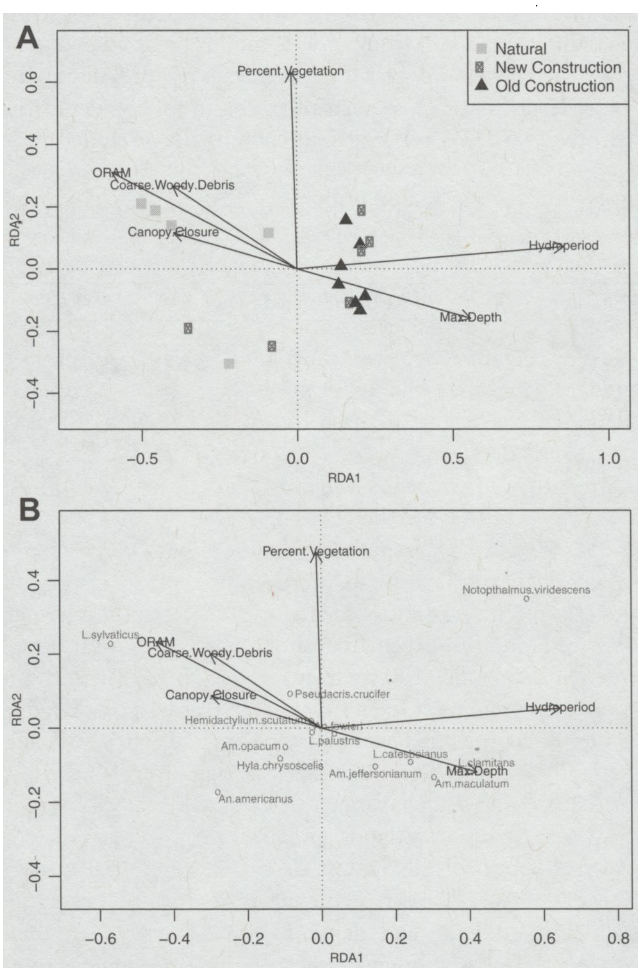

Figure 2. Redundancy analysis (RDA) triplots for (A) wetlands and (B) species abundance based on capture per unit effort in the Daniel Boone National Forest, Kentucky, May–August 2010. The proportion variance in the sample data explained by the RDA was 52%; axes 1 and 2 accounted for 66.5% and 17.3% of that total, respectively. ORAM = Ohio Rapid Wetland Assessment Method score.

(Table 5). Eastern newts were found breeding in all wetland types and best predicted by wetland type, ORAM score, maximum depth, and wetland size (Table 4). Eastern newts were negatively associated with natural wetlands and were positively associated with ORAM score and wetland size (Table 5).

The remaining 7 species that we detected could not be included in regression analyses because all of these species had low CPUE across wetland types, which precluded statistical analysis (Table 3). We only found wood frogs (*L. sylvaticus*) in natural, ephemeral wetlands and they had the greatest CPUE values of any species where they were detected. We captured all but 3 marbled salamander (*Am. opacum*) larvae in natural ephemeral wetlands. American toads (*A. americanus*) were only located in 1 natural wetland and 1 wetland of the new construction type, both of which dried during the June sampling period. Fowler's toads (*An. fowleri*), Pickerel frog (*L. palustris*), and four-toed salamanders (*Hemidactylium scutatum*) were poorly detected; hence, commentary on habitat associations is not warranted (Table 3).

DISCUSSION

Amphibian habitat conditions associated with constructed wetlands on ridge tops in the DBNF do not provide habitat conditions that support the amphibian community associated with natural, ephemeral wetlands. Constructed wetlands provide breeding habitat for predatory amphibian species that are excluded from natural wetlands in the area. Our finding is primarily a result of hydrology whereby natural wetlands are ephemeral, old construction method wetlands are permanent, and new construction method wetlands are mostly permanent. We identified 2 groups of species that associate most closely with either old construction method wetlands (predominantly large ranid frogs) or natural wetlands (predominantly wood frogs), and an additional group of species that bred in all wetland types but occurred at greater CPUE in either permanent or ephemeral hydrology (predominantly ambystomatid salamanders). Our RDA

Table 4. Tweedie regression models for amphibian abundance within constructed and natural ponds of the Daniel Boone National Forest, Kentucky, May–August 2010. Only models with a difference in Akaike's Information Criterion corrected for small sample sizes (ΔAIC_c) value ≤ 2.0 for each species are displayed.

Species	Model[a]	K[b]	Log-likelihood	AIC_c	ΔAIC_c	w_i[c]
Lithobates clamitans	Depth, size, wetland type	6	−19.01	52.64	0.00	0.49
	Wetland type, max depth	5	−21.08	53.02	0.38	0.41
Hyla chrysoscelis	Depth, size, wetland type	6	−24.25	63.11	0.00	0.51
	Wetland type	4	−28.44	64.47	1.36	0.26
	Size	2	−29.95	64.65	1.54	0.24
Pseudacris crucifer	Depth, size, wetland type	6	−18.55	51.72	0.00	0.54
	Canopy closure, depth, wetland type, size	7	−16.65	52.30	0.59	0.40
Combined *Ambystoma*	Vegetation	2	−36.06	76.88	0.00	0.47
	Depth, vegetation, size	4	−33.06	76.98	0.10	0.44
Notopthalmus viridescens	Wetland type, ORAM	5	−28.25	67.36	0.00	0.47
	Depth, size, wetland type	6	−26.67	67.96	0.60	0.35

[a] Wetland type = natural, old method construction, or new method construction; vegetation = percent cover of aquatic vegetation; ORAM = Ohio Rapid Wetland Assessment Method score.
[b] Number of parameters in the model, including the intercept.
[c] Akaike weight; can be interpreted as the probability of the model being the best fitting model.

analysis suggested that relative abundance of amphibian species is associated with multiple interacting habitat factors, providing evidence for the existence of complex gradients of habitat variables that influence amphibian presence and abundance (Skelly et al. 1999, Shulse et al. 2010). Based on regression analyses of individual species, wetland maximum depth and size were the primary predictor variables for the CPUE of green frogs, ambystomatid salamanders, and eastern newts.

Species Associations With Wetland Type and Hydrology

Wood frogs and marbled salamanders were associated with ephemeral natural wetlands, whereas green frogs and American bullfrogs associated with permanent constructed wetlands. Marbled salamanders might be excluded from constructed wetlands because this species requires fluctuating water levels that expose parts of the basin for egg deposition (Scott 2005). Wood frogs are potentially excluded from

Table 5. Model averaging of the parameters within the models with a difference in Akaike's Information Criterion corrected for small sample sizes (ΔAIC_c) value ≤ 2.0 based on Tweedie regression models of amphibian abundance within constructed and natural ponds in the Daniel Boone National Forest, Kentucky, May–August 2010.

Species	Parameter name[a]	Model-averaged estimate ($\hat{\beta}$)	Unconditional SE	85% CI[b]
Lithobates clamitans	Wetland type			
	Natural	−9.73	4.01	−15.51, −3.95
	Old construction	−0.89	1.60	−3.19, 1.41
	New construction	0.00	0.00	0.00, 0.00
	Max. depth	0.02	0.01	0.01, 0.03
	Size	0.00	0.00	−0.01, 0.00
Hyla chrysoscelis	Size	−0.03	0.04	−0.09, 0.03
	Wetland type			
	Natural	−2.73	3.13	−7.24, 1.77
	Old construction	−1.46	3.13	−5.97, 3.05
	New construction	0.00	0.00	0.00, 0.00
	Depth	−0.03	0.03	−0.07, 0.02
Pseudacris crucifer	Size	0.02	0.01	0.01, 0.03
	Depth	−0.15	0.05	−0.23, −0.07
	Wetland type			
	Natural	−8.06	4.17	−14.07, −2.05
	Old construction	3.99	3.13	−0.52, 8.50
	New construction	0.00	0.00	0.00, 0.00
	Canopy closure	0.08	0.59	−0.78, 0.93
Combined *Ambystoma*	Vegetation	−0.02	0.01	−0.03, −0.01
	Depth	0.01	0.00	0.01, 0.02
	Size	0.00	0.00	−0.00, 0.00
Notopthalmus viridescens	Wetland type			
	Natural	−5.16	1.75	−7.67, −2.64
	Old construction	−0.46	0.72	−7.67, −2.64
	New construction	0.00	0.00	0.00, 0.00
	ORAM	0.12	0.04	0.05, 0.18
	Depth	0.01	0.01	−0.01, 0.02
	Size	0.01	0.00	0.00, 0.01

[a] Vegetation = percent cover of aquatic vegetation; ORAM = Ohio Rapid Wetland Assessment Method score.
[b] We used 85% confidence intervals to make confidence intervals AIC compatible (Arnold 2010).

constructed wetlands because of egg and embryo predation by green frog larvae and adult eastern newts (Vasconcelos and Calhoun 2006). American bullfrogs and green frogs are excluded from natural, ephemeral wetlands because their larvae overwinter in Kentucky, making them unable to sustain populations in ponds that dry seasonally (Tattersall and Ultsch 2008). For some species, such as wood frogs, occupancy and CPUE were distinct (i.e., a species only present in 1 wetland type). These distinct hydrology preferences by certain species likely caused the significant difference we observed in amphibian community composition between old construction method wetlands (all permanent) and the natural wetlands (all ephemeral). New construction method wetlands included permanent ($n = 5$) and ephemeral ($n = 2$) hydrology, but the ephemeral constructed wetlands were not used by wood frogs or marbled salamanders. These ephemeral constructed wetlands excluded the large ranid species from breeding, resulting in an amphibian community more similar to natural wetlands. Hence, the amphibian community similarity between the new construction method and natural wetlands is primarily the result of excluding large ranid frogs and not the mutual occurrence of species that are primarily ephemeral breeders (e.g., wood frogs and marbled salamanders).

Species found in all 3 wetland types generally exhibited greater CPUE either in ephemeral or in permanent wetlands instead of being equally captured in all wetland types. Species that were found with greater CPUE in ephemeral wetlands (constructed and natural) included spring peepers, Cope's gray treefrogs, American toads, and Fowler's toads. Despite having a greater CPUE on average in natural wetlands, spring peepers were negatively associated with natural wetlands. This is likely because spring peepers had high CPUE in constructed wetlands that were ephemeral, indicating that wetland hydrology is a more influential predictor that other factors related to the different wetland types for this species. Although spotted and Jefferson salamanders are typically associated with ephemeral wetlands (Petranka 1998), they occurred with greater CPUE in permanent constructed wetlands in our study, along with eastern newts. The CPUE of ambystomatid salamanders in permanent wetlands in this study could be related to their preference for longer hydroperiods, ability to persist in the presence of green frogs, and lack of fish predation (Egan and Paton 2004, Porej and Hetherington 2005, Vasconcelos and Calhoun 2006). For 2 of the 3 most commonly captured amphibians (green frogs and eastern newts), CPUEs were best predicted by wetland type and positively associated with old construction wetlands. Green frogs and American bullfrogs require permanent bodies of water because of overwintering larvae and late breeding periods, and eastern newts have an affinity for deep wetlands (Gates and Thompson 1982, Casper and Hendricks 2005, Pauley and Lannoo 2005).

Species Associations With Habitat Variables

Green frogs were positively associated with wetland depth and eastern newts were positively associated with wetland size. Eastern newts can occupy habitats with predatory fish because their skin toxicity deters predation (Gates and Thompson 1982). Therefore, newts likely occurred at greater CPUE in constructed wetlands because of an adaptation that allows for tolerance of larger ranid predators. Additionally, eastern newts may occur at greater CPUE in constructed wetlands because the provision of permanent water year round reduces energy expenditure on migration (Hunsinger and Lannoo 2005). Surprisingly, we found no significant association between spring peepers and canopy closure, a species that has been well-documented in preferring wetlands with open canopies (Halverson et al. 2003) and forming population sinks in wetlands with high levels of forest canopy (Werner et al. 2009).

The CPUE of *Ambystoma* salamanders was negatively associated with the amount of wetland vegetation and positively associated with wetland depth and wetland size. The negative statistical association between spotted salamander CPUE and aquatic vegetation contrasts with results from other studies that show positive statistical associations between spotted salamander abundance and aquatic vegetation (Egan and Paton 2004, Shulse et al. 2010). However, Egan and Paton (2004) surveyed egg masses and not larvae, potentially causing a difference in association. Additionally, adult spotted salamanders were not statistically associated with amount of CWD, supporting the results of Patrick et al. (2008), who found that adult spotted salamanders equally colonized created pools with and without surrounding CWD.

Amphibian populations can vary annually in demographic characteristics (e.g., local abundance, timing of reproduction, and population size structure), which are influenced by precipitation for wetland-breeding species (Pechmann et al. 1989, Richter et al. 2003). Although our study occurred over a single breeding season, precipitation was comparable to the 40-year average. All study wetlands occurred in a relatively confined landscape of similar geology, land use, and local climate. Therefore, we assumed that large-scale fluctuations in amphibian population characteristics caused by annual weather or other environmental stressors should affect all wetlands in our study equally. Therefore, we are confident that relationships we described for amphibian populations in natural and constructed wetlands are representative of the ridge top wetland ecosystem.

Evaluation of Constructed Wetland Strategies

A greater maximum depth resulted in permanent hydroperiods for ridge top wetlands constructed in the DBNF using the old construction method. Even though the new construction method wetlands were shallower than old construction method wetlands, many (67%) had a permanent hydrology. New construction method wetlands also had more aquatic habitat structure in the form of aquatic CWD (as measured by the ORAM interspersion metric). The ORAM scores indicated that newly constructed wetlands did not provide habitat conditions similar to reference conditions. Differences between wetland types in overstory canopy closure were most likely related to forest management activities around constructed wetlands. Of the 3 wetland types, we assumed that natural wetlands had experienced the lowest level of anthropogenic disturbance. Additionally, most constructed wetlands were built as part of localized timber management activities and near forest roads, whereas the majority of natural wetlands were relatively secluded.

Natural ridge top wetlands occur at low density in the northern portion of the DBNF, relative to areas south of our study area. Creating wetlands that are more natural in ecological function has become a recent priority, but the new method of wetland construction implemented 2004–2007 has not consistently produced ephemeral wetlands, which is necessary to exclude species that depend on permanent water (e.g., green frogs, American bullfrogs) or thrive in permanent water (e.g., eastern newts). Permanent-water breeding amphibians are endemic to the DBNF; however, they were presumably confined to lowland basins where permanent marshes, oxbows, and natural lakes provided breeding habitat prior to construction of permanent wetlands on ridge tops. The large ranid frogs, especially American bullfrogs, are known to be invasive in altered aquatic habitats with permanent water (Fuller et al. 2010). Our results indicate that populations of ephemeral-breeding specialists in the DBNF such as wood frogs and marbled salamanders are predominately confined to the few natural, existing ephemeral wetlands that remain. Even though ephemeral-specialist species occur in high abundance in natural, ephemeral wetlands, confinement to natural wetlands could lead to long-term negative consequences associated with geographic isolation, including loss of genetic variability (Garner et al. 2003, Richter et al. 2009) and increased likelihood of local extinction resulting from disease, environmental stochasticity, or demographic stochasticity (Alford and Richards 1999, Semlitsch 2002, Richter et al. 2003). The propagation of permanent wetlands over the last 20 years in the DBNF has likely provided avenues of dispersal and migration for green frogs, American bullfrogs, and eastern newts, which might expose naturally occurring ridge top amphibian species to direct predation and disease, such as amphibian chytrid fungus (*Batrachochytrium dendrobatidis*) and ranavirus (Daszak et al. 2004, Gahl 2007, Gahl et al. 2009).

MANAGEMENT IMPLICATIONS

Results of this study underscore the importance of using constructed wetlands as a conservation strategy for amphibians and the need for research and monitoring on how these wetlands function. For ridge top wetlands in our ecosystem, wetland construction should include gradual slopes to a maximum depth of 25–30 cm and exclude wetland liners that prevent drainage. Constructing wetlands to ensure that water is ephemeral is the most important consideration because it is the primary driver of amphibian community composition. Our results confirm that ORAM is a valuable tool for monitoring amphibian habitats in natural and constructed wetlands. ORAM uses data from multiple habitat parameters that can denote high quality ephemeral wetland habitat (canopy cover, wetland size, and hydrology). As suggested by Semlitsch (2008), wetlands constructed for mitigation or otherwise should be built with consideration to function and quality, not quantity exclusively.

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