Herpetological Conservation and Biology 8(3):715−723.
Submitted: 4 May 2012; Accepted: 11 October 2013; Published: 31 December 2013.

Salamanders Continue to Breed in Ephemeral Ponds Following the Removal of Surrounding Terrestrial Habitat

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***Abstract.*—Forest and wetland degradation due to human disturbance is detrimental to pond-breeding amphibians that require both aquatic and terrestrial habitats to complete their complex life cycle. In this study, we examined the importance of forest cover within concentric non-overlapping terrestrial zones on amphibian reproductive effort. On the southern Cumberland Plateau, Tennessee, USA, we counted Spotted Salamander (*Ambystoma maculatum*) egg masses in February and March 2004 at 25 ephemeral ponds either surrounded by cut or uncut forest. Using regression tree analysis, we determined which of 10 local and landscape parameters (pond area, pH, temperature, maximum water depth, dissolved oxygen, canopy cover, number of ponds within 1,000 m, percent forest in 2003 within 0–164, 164–250, and 250–1,000 m) best predicted salamander egg mass densities. Egg mass densities were significantly higher at ponds within uncut forests and positively associated with forest cover at all three spatial zones measured (0–164, 164–250, and 250–1,000 m). All but two ponds with surrounding cut forests contained breeding populations of *A. maculatum* even though the majority of the core terrestrial zone was highly disturbed. Our data suggest that ephemeral ponds with disturbed core terrestrial habitats are still used by salamanders for breeding. Despite the obvious importance of preserving forest habitat around wetlands, the complete loss of amphibian populations following extensive terrestrial habitat loss may be prevented by retaining aquatic habitats and forest cover at exterior spatial zones.**

Key Words.—*Ambystoma maculatum*; conservation; management; pond-breeding amphibian; Spotted Salamander; terrestrial habitat

Introduction

Ephemeral pond systems are distributed throughout the world and provide habitat for diverse bird, mammal, invertebrate, and amphibian communities (Leibowitz 2003; Tiner 2003a, b; Colburn 2004; Scheffers et al. 2006). Because of their small size and hydrologic isolation, the ecological importance of ephemeral ponds is frequently overlooked by developers, land managers, and policy makers (Haukos and Smith 2003). Human modifications of the landscape, including the alteration, fragmentation, and loss of both wetland and terrestrial habitats, have reduced wetland biodiversity (Gibbs 1993; Semlitsch 1998; Semlitsch and Bodie 1998; Guerry and Hunter 2002; Scheffers and Paszkowski 2012). This is particularly true for pond-breeding amphibians as many of these species display life histories that depend on both aquatic and terrestrial environments (Semlitsch 1998; Semlitsch and Bodie 1998; Porej et al. 2004; Gamble et al. 2006; Becker et al. 2007).

Core terrestrial habitat ranging from just 30 m to up to 250 m surrounding breeding wetlands may contain up to approximately 95% of the local ambystomatid populations (derived from several species of *Ambystoma* salamanders; Semlitsch 1998; Rittenhouse and Semlitsch 2007) and is considered essential for population persistence through time (Porej et al. 2004; Greenwald et al. 2009). Semlitsch (1998) suggested that intact terrestrial habitat within 164 m of breeding wetlands was required to protect the primary habitat used by ambystomatid salamanders. Disturbance to this area may decrease species occurrence, abundance, and richness (Guerry and Hunter 2002; Homan et al. 2004). Little is known, however, regarding the importance of intact forest outside the core habitat area, particularly when core habitat is disturbed (Semlitsch et al. 2009; Veysey et al. 2009). In the present study, we examined the importance of terrestrial habitat zones surrounding ephemeral ponds for breeding populations of Spotted Salamander, *Ambystoma maculatum*, on the Cumberland Plateau, Tennessee, USA.

The objective of our study was to compare ephemeral wetlands with cut and uncut surrounding forest to determine if ponds with disturbed core terrestrial habitat (i.e., within 164 m) are capable of supporting breeding salamander populations. To do this we compared whether salamander populations are present at ponds within cut and uncut forests and address whether *A. maculatum* reproductive effort (measured by egg mass density) is associated with the amount of forest cover in the surrounding terrestrial habitat. We also compared within-wetland environmental variables between ponds within cut and uncut forests in order to determine what other factors may be influencing salamander reproduction.

Materials and Methods

Study area.—Our study area was a 248,500 ha portion of the Cumberland Plateau in Franklin, Grundy, Marion, Sequatchie, and Van Buren counties, Tennessee (Fig. 1). Upland forests are

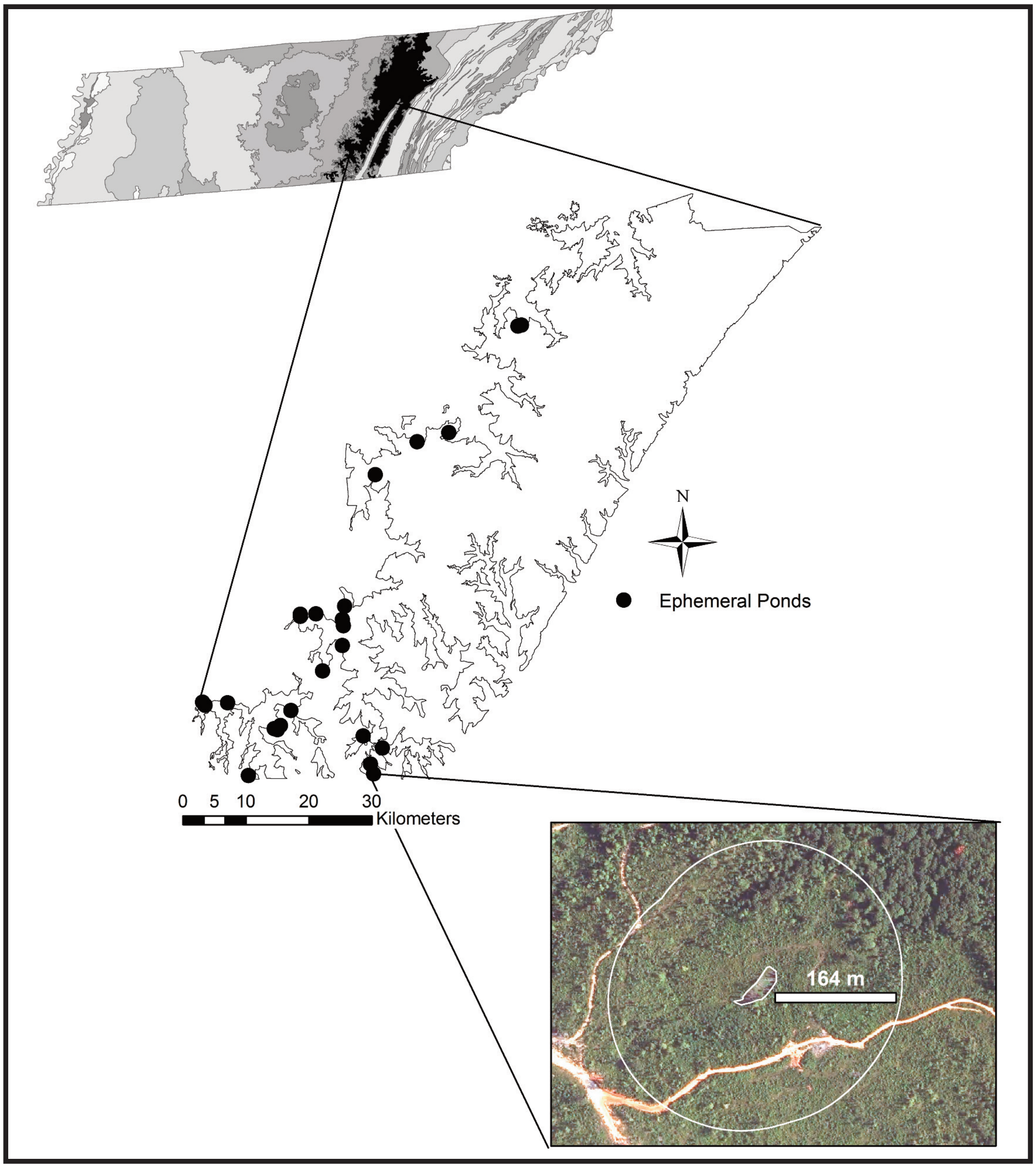

Figure 1. Distribution of 25 ephemeral ponds located on the southern Cumberland Plateau, Tennessee. Polygons in grey scale within the state of Tennessee show various ecoregions with larger blown-up polygon indicating the extent of the Cumberland Plateau within Tennessee (http://www.epa.gov/wed/pages/ecoregions/tn_eco.htm [Accessed 8 April 2011]). Aerial photo (lower right corner) represents an example of a cut ephemeral pond (forest loss within 164 m). (Photograph from National Agriculture Imagery Program).

dominated by second growth oak (*Quercus* spp.) and hickory (*Carya* spp.; Reid et al. 2008). The pond hydroperiod generally follows an annual cycle with surface water present between November and June (Corser 2008). Variation may exist in pond hydroperiod across the entire extent of the Cumberland Plateau. However, all ponds surveyed in our study were observed to dry annually, and none contained fish (Brett R. Scheffers and Jonathan E. Evans, unpubl. data). Being the only naturally occurring bodies of water on the surface of the Plateau, ephemeral ponds are essential in supporting 18 of the 21 pond-breeding amphibian species known to occur in the region.

The forests of the Cumberland Plateau have undergone a dramatic shift in composition as a result of urban sprawl and conversion to intensively managed pine plantations (McGrath et al. 2004). Of the 14% hardwood forest cover on the Plateau lost since 1981, 74% resulted from hardwood-to-pine conversion (McGrath et al. 2004). Additionally, 70% of forest removal from 1997 to 2000 on the Cumberland Plateau resulted from clear-cutting parcels greater than 48.6 ha in size (McGrath et al. 2004). Such forestry practices resulted in significant losses of forest cover within 164 m of ephemeral ponds since 1981 (Brett R. Scheffers and Jonathan E. Evans, unpubl. data).

Forest cover and egg mass surveys.—We conducted egg mass surveys at 30 ephemeral ponds with two types of forest cover conditions within 164 m of the pond: 14 ponds predominantly surrounded by forest (~90%; hereafter "uncut ponds"); and 16 ponds with little to no forest canopy cover (~20%; hereafter "cut ponds"). These ponds were randomly selected from a database of ephemeral pond localities from our study area (the Landscape Analysis Lab, Sewanee, Tennessee). We chose ponds that met our above criteria for surrounding forest cover and were accessible.

We excluded five of the 30 ponds surveyed from all analyses because of factors that made them unsuitable for comparisons: earth-moving equipment partially filled three cut ponds, soil erosion obstructed visibility at another cut pond, and paint cans and car batteries polluted one uncut pond. Thus, the final analysis included 13 uncut and 12 cut ponds.

We differentiated the two types of forest cover conditions by quantifying the percent forest cover surrounding our survey ponds using 2003 digital layers in a Geographical Information System (GIS; all digital layers of forest cover used in this study were created by and are property of the Landscape Analysis Lab, Sewanee, Tennessee [McGrath et al. 2004]).

We began egg mass counts on 22 February 2004, immediately following the first signs of breeding by *A. maculatum*, and concluded on 10 March 2004. To minimize temporal bias, we alternated surveys between ponds with cut and uncut surrounding forests. We conducted surveys by systematically wading through ponds and visually counting egg masses with large clusters of masses being taken as the average of three counts (Petranka et al. 2003; Baldwin et al. 2006). Below-surface clusters were counted by feeling for each mass. We obtained egg mass density by dividing the total count for a pond by its total area (m^2).

We used GIS to quantify percent forest cover within three spatial zones: 0–164, 164–250, and 250–1,000 m. Non-nested zones (i.e., 0–164 m, 164–250 m, etc.) were used instead of the traditional nested zones (e.g., 0–164 m, 0–250 m, etc.) in order to increase independence amongst each zone (Scheffers et al. 2012). We chose a distance of 164 m from pond edge as this distance contains approximately 95% of ambystomatid populations (Semlitsch 1998). We chose a 164–250 m zone because terrestrial habitat used by 95% of ambystomatid salamanders extends up to 245 m from breeding sites (Rittenhouse and Semlitsch 2007), and Herrmann et al. (2005) found *A. maculatum* larval densities were significantly associated with amount of forest within 250 m of wetland breeding sites. We chose a 250–1,000 m zone because a distance of 1,000 m from the pond edge is the estimated maximum dispersal distance of *A. maculatum* (Smith and Green 2005).

Environmental variables.—We determined which of six local parameters (pond area, pH, temperature, maximum water depth, dissolved oxygen, and canopy cover) and four landscape parameters (number of ponds within 1,000 m, and percent forest in 2003 within 0–164, 164–250, and 250–1,000 m) best predicted salamander egg mass densities. We compared within-pond variables to assess potential confounding factors on salamander oviposition. At the center of each pond, we used a calibrated

Hydrolab Quanta water chemistry meter (Hydrolab Corporations, Loveland, Colorado, USA) to measure water pH, surface water temperature, dissolved oxygen, and conductivity (SpC). Measurements were taken approximately 30 cm below the water's surface from 1200–1600.

Above-pond canopy cover was delineated in GIS. We used 1997 National Aerial Photography Program (Digital Ortho Quarter Quads (DOQQ) at 1-m resolution, leaf-off) and 2006 and 2007 NAIP (National Agricultural Imagery Program, at 1-m pixel resolution natural color aerial photos, leaf-on) imagery to quantify canopy cover. We mapped ponds with 1997 DOQQ aerial photos under leaf-off conditions in order to derive pond area unobstructed by canopy cover. We superimposed 1997 pond area onto leaf-on 2006 and 2007 NAIP imagery and mapped all gaps in canopy cover for each pond. All major gaps in canopy were identified by black or dark pixels representative of water reflection or distinct physical or vegetation cover types other than canopy (Blackburn and Milton 1996). We determined canopy cover by subtracting canopy gaps from total pond area. All geospatial analyses were completed using the ArcGIS 9.3 software package (Esri, Redlands, California, USA).

Data analysis.—We used one-way Analyses of Variance (ANOVA) to assess differences in egg mass counts, egg mass density, pond area, pH, temperature, maximum water depth, dissolved oxygen, canopy cover, number of ponds within 1,000 m, and percent forest in 2003 within 0–164, 164–250, and 250–1,000 m between cut and uncut ponds. We used a Tukey's multiple comparison test to determine whether differences existed in percent forest cover for each concentric spatial zone within cut and uncut pond categories.

The relative importance of each variable in predicting egg mass density was determined using regression tree analysis. We used Breiman's random forest algorithm from the package *randomForest* in R stats version 2.15.1 (R Project for Statistical Computing, http://www.r-project.org [accessed 16 October 2012). We constructed unbiased forest of 1,000 trees following an adjusted parameter setting suggested by Strobl et al. (2007) and Breimen (2001). We set the number of variables sampled for splitting at each node (mtry) to two and the node size to one. We chose a random forest analysis because it allows for more variables than samples, is robust to interactions and correlations among variables, and does not over fit the data (Ranganathan and Borges 2010). We used the following predictor variables in this analysis: a factor for cut and uncut ponds (TYPE), pH, maximum water depth (DEPTH), water temperature (TEMP), dissolved oxygen (DO), specific conductance (SpC), canopy cover (CC), number of ponds within 1,000 m (Ponds1000), forest (% cover) from 0–164 m (NF164), forest from 164–250 m (NF250), and forest from 250–1,000 m (NF1000). Our response variable was egg mass density. We generated a variable importance value for each predictor variable. Random forest deciphers how much prediction error changes when out-of-bag data for that variable is permuted while all others are left unchanged (Breiman 2001) and designates for each variable the percentage increase in the mean square errors (%IncMSE) relative to all predictors. In other words, we record the changes in mean square error that is realized by leaving a variable out of the model. Lastly, we further validated our models by comparing the importance of original attributes based on z-scores to values derived from randomization using the iterative learning *Boruta* function in the Boruta package in R 2.15.1.

Shapiro-Wilk test and Levene's test were used to test for normality and equal variances. To achieve normality of data, we $\log_{10}$-transformed pH, arcsin transformed percent forest cover for all three spatial zones and canopy cover, and square-root transformed egg mass density and number of ponds within 1,000 m.

Time did not influence oviposition, as egg mass abundances were not correlated with time in a Pearson correlation matrix. Furthermore, we used egg mass density as opposed to egg mass counts to account for potential capacity biases due to pond area. All statistical analyses were conducted in R stats version 2.15.1.

Results

We found *A. maculatum* egg masses at 23 of 25 (92%) surveyed ponds; two cut ponds did not have egg masses present. We counted a total of 2,598 egg masses (mean ± SD = 200 ± 40, min = 44, max = 584) within 13 uncut ponds and 852 egg masses (mean ± SD = 71 ± 29, min = 0, max

= 354) within 12 cut ponds. Similarly, egg mass densities averaged 0.23 egg masses/m² (± 0.15, min = 0.04, max = 0.52) at uncut ponds compared to 0.09 egg mass/m² (± 0.14, min = 0, max = 0.52) at cut ponds.

Egg mass counts and densities, percent canopy cover, and percent surrounding forest within 164 m, 164–250, and 250–1,000 m zones were significantly different between cut and uncut ponds ($P < 0.001$); however, no statistical differences between cut and uncut ponds were found in pond area, water pH, maximum pond depth, water temperature, dissolved oxygen, conductivity, and number of ponds within 1,000 m (Table 1). At cut ponds, percent forest cover was significantly lower within the 0–164 m zone than the 250–1,000 m zone (Tukey's multiple comparison tests, $P = 0.004$) whereas it did not differ between the 0–164 m and 164–250 m zone nor between the 164–250 m and 250–1,000 m zones (Tukey's multiple comparison tests, $P = 0.375$ and $P = 0.109$, respectively). No differences existed in forest cover between any of the uncut spatial zones (all $P > 0.05$).

The variable importance ranking generated by the random forest analysis showed that forest cover within 164 m was the most important predictor of egg mass density according to the percentage increase in the mean square errors (9.9%) followed by forest cover between 164 and 250 m (7.8%) and between 250 and 1,000 m (5.1%; Fig. 2). According to our analysis of z-scores, all three zones were confirmed as important predictors. Wetland type increased the mean square errors (4.9%) but was not confirmed as an important predictor according to its z-scores. Our models explained 7% of the variance.

Discussion

We found that Spotted Salamanders continue to breed at ponds despite extensive removal of surrounding forest habitat. We found several ponds with less than 35% forest cover across all spatial zones that had higher egg mass densities than completely forested uncut ponds. In fact, all but two cut ponds had egg masses present even though the 0–164 m zone averaged 17% forest cover compared to 90% at uncut sites. These data suggest that Spotted Salamanders exhibit certain levels of resilience to habitat disturbance within the core terrestrial zone.

Historical land use may influence breeding site

Table 1. Environmental and landscape variables measured at 25 ephemeral ponds. Table displays mean ± SD and results for ANOVA between cut and uncut ponds. SpC represents specific conductance of water.

	Egg mass counts	Egg mass density (egg mass/m²)	Pond area (m²)	Water pH	Water depth (m)	Water Temperature (°C)	Dissolved Oxygen	SpC (µS/cm)	Canopy cover (%)	Ponds within 1,000 m	2003 Forest 0–164 (%)	2003 Forest 164–250 (%)	2003 Forest 250–1000 (%)
Uncut	200 ± 40	0.22 ± 0.15	989 ± 124	5.06 ± 0.36	0.74 ± 0.15	9.90 ± 1.98	8.40 ± 1.81	0.02 ± 0.003	78 ± 5	2 ± 0.44	90 ± 3	96 ±3	91 ±2
Cut	71 ± 29	0.08 ± 0.15	1024 ± 106	5.20 ± 0.57	0.72 ± 0.24	10.98 ± 2.85	7.76 ± 1.89	0.02 ± 0.003	58 ± 8	3.25 ± 0.97	17 ± 4	31 ±8	48 ±7
ANOVA	0.006[a]	0.034[a]	0.815	0.511	0.44	0.374	0.37	0.890	0.024[a]	0.245	<0.0001[a]	<0.0001[a]	<0.0001[a]

[a]denotes signficant p-values (α < 0.05)

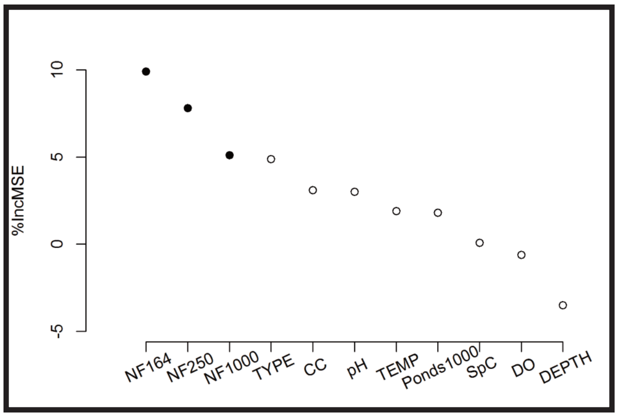

FIGURE 2. The best predictors of *Ambystoma maculatum* egg mass densities, based on percentage increase of mean square errors (%IncMSE), for all ponds combined. Variables with positive %IncMSE are better predictors of *A. maculatum* egg mass densities than variables with negative %IncMSE. Variables on x-axis are defined in text. Solid points indicate confirmed important variables by z-score analyses. For random forest analysis, the mean square error is computed on the out-of-bag data for each regression tree, and then the same computed after permuting a variable. The differences are averaged and normalized by the standard error.

selection as well as recovery of amphibian populations (Baldwin et al. 2006). We note that the forests surrounding six of the cut ponds in our study were first disturbed between 1990 and 2000 and contained on average 63 (± 63) egg masses per pond in 2004. This is similar to those ponds disturbed post-2000, which contained on average 79 (± 134) egg masses per pond. Thus, salamanders continue to breed at ponds independent of time; even wetlands that had forest cut within 0–164 m as early as 1990 still had breeding populations 14 years later.

The amount of core terrestrial habitat for pond-breeding amphibians differs among species from a few hundred square meters (Scheffers et al. 2012; Scheffers and Paszkowski 2013) to thousands (Homan et al. 2004; Porej et al. 2004; Herrmann et al. 2005; Rittenhouse and Semlitsch 2007). Egg mass densities were positively associated with the amount of forest cover within all three spatial zones considered in our study. Ponds that had forest removed within the core area experienced, on average, a 65% reduction in egg masses in comparison to ponds with forested core areas. Although we observed breeding effort at wetlands with forest cut 14 years earlier, such a reduction in reproductive effort may make breeding populations vulnerable to stochastic events such as drought and unusually cold over-wintering temperatures (Taylor et al. 2005). Connectivity between upland/terrestrial habitat and breeding habitat is an important feature influencing breeding success in Spotted Salamanders (Greenwald et al. 2009). We suspect this is also true for populations found in our study area. Thus, forestry practices that preserve aquatic but not core terrestrial habitat may not be sufficient to maintain large *A. maculatum* populations (Findlay and Houlahan 1997; Herrman et al. 2005; Rittenhouse and Semlitsch 2006).

We used 164 m as the inner zone in our analysis because of its ecological importance to *Ambystoma* salamanders. The importance of the 0–164 m zone and the two outer zones (164–250 m, 250–1,000 m) in predicting egg mass density may be due to spatial correlation in forest cover data between zones, but also because salamanders travel large distances and use areas far away from their breeding wetlands (Smith and Green 2005). Our study highlights the importance of core terrestrial habitat within 164 m of pond edge in maintaining the presence and productivity in breeding; however, our data do not provide sufficient support to recommend a distance of 164 m as a threshold distance for conservation.

Management and conclusions.—Wetlands as small as 500 m^2 provide critical breeding habitat for pond-breeding amphibians in the northeastern USA and on the northern Cumberland Plateau (Egan and Paton 2004; Denton and Richter 2013). Our ponds, which are of comparable size (800–1200 m^2), are the only naturally occurring wetlands on the southern Cumberland Plateau (Brett R. Scheffers, unpubl. data) and are extensively used by Spotted Salamanders and other amphibians (Scheffers 2010). The small size of these wetlands makes their conservation challenging as the ecological importance of these small ponds is often overlooked in land management and planning (Semlitsch and Bodie 1998).

Ephemeral ponds with disturbed core terrestrial habitats have value for amphibian populations. We found that retaining some forest within 1,000 m of breeding wetlands may allow ponds to continue to be used as breeding habitat, as the upland forested habitat regrows. Therefore, conserving widely distributed populations across the landscape might be accomplished by retaining intact pond habitats, maintaining non-converted secondary regrowth as well as increasing the amount of undisturbed forest within 1 km of these ponds (Marsh and Trenham 2000).

Acknowledgments.—Funding was provided by the University of the South through an Environmental Studies grant and Jesse Ball DuPont grant. We thank the Biology Department and the Landscape Analysis Lab at the University of the South for providing logistical support. We thank Edward Carlos, Erin Bayne, Connie Browne, Justin Hanisch, Bert Harris, Nick Hollingshead, Eva Kuczynski, Diane Orihel, Leighton Reid, Tracy Rittenhouse, Kim Rondeau, Rebecca Rooney, and Cindy Paszkowski for advice and support on this manuscript.

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Scheffers et al.—Continuation of salamander breeding after surrounding habitat removal.