THE IMPORTANCE OF NATURAL HISTORY, LANDSCAPE FACTORS, AND MANAGEMENT PRACTICES IN CONSERVING POND-BREEDING SALAMANDER DIVERSITY

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Abstract.—I have analyzed presence, abundance, and patterns of coexistence of 11 species of pond-breeding salamanders from 203 managed sites in Indiana, Illinois, Kentucky, Michigan, and Ohio. Among these include 47 long-term sites that have been monitored for 7–15 years. The two most abundant species, *Ambystoma tigrinum* and *A. texanum*, use open habitats such as grasslands and savanna, and are found in single species communities significantly more often than expected by a null model. Several other species were more likely to coexist with certain species in assemblages, and communities of four or more species occurred significantly more often than predicted by null models. All of the sites with four or more species have fishless seasonal or semi-permanent wetlands and forested upland habitat. Among populations with long-term data, five species declined at some sites and two species increased at some sites, however, most population dynamics were apparently stable fluctuations. The declining species were primarily found in mature forest upland habitat and typically breed in fishless seasonal wetlands, whereas the increasing species use open upland habitats and semi-permanent to permanent wetlands. Regression and General Linear Models indicate that the timing of prescribed burns was a significant factor in determining the relative abundance of pond-breeding salamander larvae. Prescribed burns during spring had a negative affect on the relative abundance of nine of the 10 species that I examined; the exception was the obligate aquatic salamander *Siren intermedia*. The forest dwelling species took a mean of 4.6 years for populations of these species to recover to pre-burn levels. Prescribed burns also negatively affected *Ambystoma tigrinum*, *A. texanum*, and *Notophthalmus viridescens*, however, their mean time to recover was just 1.6 years and they typically exceeded pre-burn abundance. Conservation management practices should avoid using frequent springtime prescribed burning of wetlands and surrounding upland habitats when pond-breeding salamanders are present.

Key Words.—habitat management; landscape ecology; long-term monitoring; meta-analysis; metapopulations; population trends; salamanders.

INTRODUCTION

Salamanders have a diversity of life-history adaptations that contribute to a variety of important ecological functions (Morin 1987; Fauth and Resetarits 1991; Davic and Welch 2004; Regester and Whiles 2006; Regester et al. 2006). However, salamanders are experiencing worldwide declines leaving half of all salamander species threatened with extinction (Wake 1991; Houlahan et al. 2000; Stuart et al. 2004; IUCN et al. 2008). Our knowledge of the natural history and ecology of many salamander species remain deficient. Long-term field studies at large spatial scales that focus on behavior, natural history, community structure, and population dynamics are essential for conservation efforts and monitoring programs to assess habitat management (Spellerberg 1991; Cody 1996; Storfer 2003; Milne and Bennett 2007; Semlitsch 2008). A focus on natural history of multiple life-history stages during long-term studies increase the likelihood of observing rare events, the results of slow processes, and identifying important factors that affect population dynamics and community structure (Cody 1996; Diamond 1996; Daszak et al. 2005; Whiteman and

Wissinger 2005). While there have been a number of long-term studies on salamander population dynamics (Pechmann et al. 1991; Cody 1996; Semlitsch et al. 1996; Brodman 2002; Brodman 2009a), few have focused on entire assemblages at large scales, for more than a few consecutive years, and include methods to detect all stages of the life cycle (Brodman 2009b). Short-term amphibian declines might be due to habitat degradation or they might be part of a natural cycle of population fluctuations due to abiotic and biotic causes (Pechmann et al. 1991; Cortwright 1998; Daszak et al. 2005). Studies need to be at least seven consecutive years to detect biologically meaningful trends of amphibian populations and life history and to examine the importance of abiotic and biotic factors that affect population dynamics and community structure (Sexton et al. 1998; Joseph Pechmann, pers. comm.).

Factors that influence the abundance and species richness of pond-breeding amphibians include annual variation in climate, landscape factors such as hydrology and distance between potential breeding ponds, pollution, habitat fragmentation, and land management practices (Blaustein and Bancroft 2007; Brodman

2009b). Besides the need to reproduce in wetlands, most pond-breeding salamanders depend on upland forests for foraging, hibernation, and migration (Petranka 1998; Guerry and Hunter 2002), so habitat management needs to consider impacts on salamanders across multiple landscape factors. Timber management and prescribed burns on the core of upland habitat is predicted to have negative impacts on forest species (deMaynadier and Hunter 1999; Patrick et al. 2006; Chambers 2008). Pond-breeding salamanders are predicted to do best in metapopulations within landscapes that have large clusters of wetlands that are made up of breeding site choices with varying hydrology (Lannoo 1998; Semlitsch and Bodie 1998; Brodman 2009b). Two factors combine to explain this. Sink populations within a metapopulation can function as corridors linking migration between distant source populations (MacArthur and Wilson 1967; Semlitsch and Bodie 1998; Naugle et al. 2005). A variety of ephemeral, seasonal, semi-permanent, and permanent wetlands that are available to a metapopulation offering alternating benefits depending on climatic variability from year to year (Lannoo 1998; Semlitsch and Bodie 1998).

Here I report population and community trends of 11 species of pond-breeding salamanders in a meta-analysis of 47 long-term and 156 short-term surveys of populations that I conducted in Indiana, USA, and surrounding states. The first set of objectives of this study is to use the whole data set to determine assemblage associations among salamander species, and to investigate the roles of hydroperiod heterogeneity and clustering among potential breeding sites as factors explaining salamander abundance diversity to test the hypothesis that pond-breeding salamanders are more abundant in larger wetlands clusters with varying hydrology. The second set of objectives is to use the long-term data set to determine population trends, and to test for the effect of habitat management (springtime prescribed burns) on the abundance of pond-breeding salamanders at breeding sites. Because of the large number of sites and duration of the study, these data will fill an important gap in our understanding of population and community dynamics.

MATERIALS AND METHOD

Salamander surveys.—From 1988 to 2008, I conducted surveys of pond-breeding salamanders at 203 breeding sites in Ohio, Indiana, Illinois, Kentucky, and Michigan, USA (Fig. 1). All of the sites were within actively managed natural resource reserves or nature preserves. I did not survey every site every year and I surveyed many sites during just one year. However, I collected long-term data on 47 of these 203 sites. I define long-term sites as those that I surveyed for at least seven consecutive years. Studies of shorter

duration can be useful to address questions on a spatial scale, but they are not sufficient to determine meaningful population trends (Gibbons et al., 1997; Sexton et al. 1998; Joseph Pechmann pers. comm.). Although I surveyed sites for varying numbers of years, I surveyed all sites using the same protocol. I visited each site once a month for three months during the spring season and once during the summer or fall. During each visit, I used methods targeted to certain life-history stages to increase detectability of each species. I used time-constrained methods and spent 1–10 person-hours per visit per site depending on the size and complexity of the habitat, and the number of field assistants with me. For small ponds (< 0.25 ha), the entire pond and adjacent upland habitat within 50 m of the pond was searched. For larger ponds, I searched along transects. For each population I categorized relative abundance on an ordinal scale from 0 to 5 based on the life-history stage with the highest value during a given field season. I developed the scale in a previous study (Brodman 2003) by creating formulas to equate relative abundance of different life stages collected by a variety of methods to the Karns (1986) frog call index. I used visual searches for adults under cover objects and in ponds during and after the breeding season, and for each site, I calculated the relative abundance of adults salamanders as ln (450 x captures/person-h). After the breeding season, I used visual searches, minnow traps, dipnets, and seines to sample egg masses and larvae. I calculated the relative abundance of egg masses and larvae as ln (5 x captures/person-h) using dipnets or seine, and as ln (35 x captures/trap-d) using minnow traps. All calculated relative abundance values below 1 were rounded up to 1 if at least one animal was encountered and all values greater than 5 were rounded down to 5 to create an ordinal relative abundance scale from 0−5.

I identified most salamanders in the field and immediately released them at the point of capture.

FIGURE 1. Map of study area. The counties in which surveys took place are shaded gray.

However, unisexual salamanders cannot be identified in the field. Unisexual populations of *Ambystoma* are a monophyletic and ancient lineage of all female populations that can only reproduce by stealing sperm from males of coexisting sexual species (Bogart et al. 2007; Bi et al. 2008). The coexisting sexual species in this complex are *A. texanum* (Smallmouth Salamander), *A. tigrinum* (Tiger Salamander), *A. laterale* (Blue-spotted Salamander), and *A. jeffersonianum* (Jefferson Salamander). Unisexual salamanders are currently not assigned species status because of their genetic complexity (Petranka 1998; Phillips and Mui 2005) and their biotypes are identified and distinguished from coexisting species by their genomic combination of chromosomes (L = *A. laterale*, J = *A. jeffersonianum*, T = *A. texanum*, and Ti = *A. tigrinum*). When I found populations that might include unisexuals, I took up to 20 eggs, each from a different egg mass, for allozyme analysis. I also snipped tail tips of adults and larvae for microsatellite analysis. James Bogart conducted the allozyme and microsatellite analyses at University of Guelph. For salamanders, I took tail tips in the field and I immediately released them at the site of capture. Bogart raised the eggs to metamorphosis and after analysis returned the specimen to me as vouchers, which are stored at Saint Joseph's College.

Community associations.—I used the entire data set of 203 sites to address questions about species composition in the pond-breeding salamander assemblages. I used Stepwise Regression to model the influence of each species as predictors of salamander abundance and species richness of remaining species. I used Chi-square to test for differences in observed patterns of species richness compared to expected patterns from a null model. The null model assumed that species assemblages were random based on the frequency of the occurrence of each species within their range. For example, if a set of sites occur within the range of three species, then the expected frequency of sites with two species is the sum of the occupancy of the first species times the occupancy of the second species, times 1- the occupancy of the absent species.

Although I treat unisexual salamanders as a species in the context of community analysis, I also further examined the assemblage of species that coexist with each unisexual biotype. I set significance at the 0.05 level for these and all following statistical test.

Landscape variables.—I used the entire data set of 203 sites to test questions about the influence of landscape factors on salamander abundance and species richness. I modeled two landscape factors, (1) the degree of wetland clustering and isolation, and (2) hydroperiod heterogeneity to explain salamander abundance and species richness. I detected wetland

clusters using Geographic Information System (GIS) analysis by creating 200 m core upland habitat around each wetland. I joined wetlands within overlapping core upland habitat to form wetland clusters. The rationale for this is that wetlands within 400 m have overlapping populations in the terrestrial environment (Semlitcsh 1998; Brodman et al. 2003; Brodman 2009b). The degree of wetland clustering and isolation was determined by the number of wetlands within a cluster (Brodman 2009b). This value would always be one for an isolated wetland, two for small clusters (2–13 wetlands), and high for larger clusters (14 or more wetlands). I used field observations and National Wetland Inventory Maps to characterize the hydroperiod of potential breeding ponds as seasonal, semi-permanent, or permanent. For the purpose of this study, I included ephemeral or saturated wetlands within the seasonal wetland category. I considered hydroperiod heterogeneity as high when a wetland cluster had wetlands in all three hydroperiod categories (seasonal, semi-permanent, and permanent), and low when a cluster only had one type of hydrology or if the wetland was isolated. I used MANOVA followed by the Tukey HSD post-hoc test to analyze the effects and interaction of wetland cluster size and hydroperiod heterogeneity on salamander abundance and species richness.

Population trends.—I used the subset of 47 long-term sites to address population trends. Partial data sets of some of these populations from Jasper and Newton Counties, Indiana, and Summit County, Ohio, have been previously published (Brodman and Kilmurry 1998; Brodman 2002; Brodman 2003; Brodman et al. 2005; Brodman 2009a). However, to analyze long-term trends, I included these data sets as part of the meta-analysis. I used Kendal's Tau to detect non-parametric correlations of relative abundance and time.

Occupancy is normally measured as the proportion of sites occupied by a species; however, occupancy models require estimates of detectability (MacKenzie et al. 2002). The methods of this survey were developed before the advent of occupancy models and do not meet all of the assumptions of occupancy models within a sampling season. Therefore, for the purpose of this study, I estimated detectability as the percentage of years that I detected a species at a site, and I define occupancy as the percentage of sites at which I detected a species at least once, from the subset of sites surveyed within the range of the species.

Habitat management: springtime prescribed burns.—I made note of visits that occurred shortly after prescribed burns on habitat within 200 m of the breeding ponds. I used ANOVA on the subset of 47 long-term sites to test the effects of springtime prescribed burns on population abundance. To do this, I compared relative

TABLE 1. Checklist of species of pond-breeding salamanders in Illinois, Indiana, Kentucky, Michigan, and Ohio, USA, indicating the number of populations found and occupancy estimates for each species. Occupancy is the percentage of sites present within the range of the species.

Species	Populations	Occupancy
Ambystoma tigrinum (Tiger Salamander)	103	53
A. laterale (Blue-spotted Salamander)	65	62
A. texanum (Small-mouthed Salamander)	65	53
Unisexual *Ambystoma*	37	41
A. maculatum (Spotted Salamander)	28	22
Notophthalmus viridescens (Eastern Newt)	24	15
A. opacum (Marbled Salamander)	20	31
A. jeffersonianum (Jefferson Salamander)	15	46
Siren intermedia (Lesser Siren)	15	15
Hemidactylium scutatum (Four-toed Salamander)	3	3
A. talpoideum (Mole Salamander)	2	10

abundance in the year prior to the burn to the year after the burn, and the mean number of years post-burn that it took populations to recover to pre-burn levels.

RESULTS

Salamander surveys.—I found all 11 species of pond-breeding salamanders that are known from the study area (Fig. 2). Eight of the species are ambystomatid salamanders (Table 1). The other species include one plethodontid, *Hemidactylium scutatum* (Four-toed Salamander), one salamandrid, *Notophthalmus viridescens* (Eastern Newt), and one sirenid, *Siren intermedia* (Lesser Siren). The most common species were *A. tigrinum, A. texanum,* and *A. laterale*. I found each of these species at more than 60 sites and at greater than half of the sites sampled within their geographic range (Table 1). I found that *A. tigrinum* was often the only species using farm ponds or breeding-sites adjacent to cultivated fields, and that their occupancy was lowest in the southeastern section of the study area. I found that *A. texanum* was often the only species breeding in shallow ephemeral wetlands at depths of just 10–20 cm, and that their occupancy was lowest in the northeastern part of the study area. Occupancy was greatest for *A. laterale* (Table 1). Six species, unisexual *Ambystoma*, *A. maculatum* (Spotted Salamander), *N. viridescens*, *A. opacum* (Marbled Salamander), *A. jeffersonianum*, and *S. intermedia* were uncommon. I found each of these species at 15–30 sites and 15–40% of the sites sampled within their geographic ranges. The rarest species were *H. scutatum* and *A. talpoideum* (Mole Salamander), each found at three or fewer sites with occupancy of 10% or less (Table 1).

Community associations.—Regression models indicated that the abundance of *N. viridescens*, unisexual salamander, and *A. maculatum* explained 49.8% of the variation in total salamander abundance ($r = 0.705$, $F_{3, 178} = 58.0$, $P < 0.001$), and 43.6% of the variation in salamander species richness among sites ($r = 0.660$, $F_{3, 178} = 45.1$, $P < 0.001$). The models were strengthened by including *A. tigrinum* as an indicator of salamander abundance ($r = 0.775$, $F_{4, 178} = 65.6$, $P < 0.001$), and *A. laterale* as an indicator of salamander diversity ($r = 0.757$, $F_{4, 178} = 46.6$, $P < 0.001$).

Breeding sites with just one species (95 sites) occurred significantly more often than expected by the null model (62.9; $\chi^2 = 23.16$, df = 1, $P < 0.001$). Two-thirds of these sites had only *A. tigrinum* or *A. texanum* (Table 2), and these were the only species that were more frequently the only species at a site than expected by chance (*A. tigrinum* $\chi^2 = 10.33$, df = 1, $P < 0.001$; *A. texanum* $\chi^2 = 26.81$, df = 1, $P < 0.001$). I found 12 sites with four or five species (Table 2) and this was significantly more often than expected ($\chi^2 = 2181.9$, df = 1, $P < 0.001$), whereas 57 sites with two species ($\chi^2 = 17.25$, df = 1, $P = 0.024$) and 36 sites with three species ($\chi^2 = 5.12$, df = 1, $P = 0.024$) were found significantly less often than expected. Regression models found predictor species that explain some of the variation in the abundance of most pond-breeding salamanders. The predictor species primarily had one to several positive and negative associations among pairs of *Ambystoma* species and between *Ambystoma* and *N. viridescens* (Table 3). Among the positive relationships were those between *N. viridescens* and *A. tigrinum, A. texanum, A. laterale, A. maculatum,* and *A. opacum,* those between *A. jeffersonianum* and *A. opacum* and unisexual salamanders, and those between *A. talpoideum* and *A. opacum* and *A. texanum* (Table 3). Negative relationships primarily involved *A. tigrinum* or *A. texanum*. There were no significant associations of species pairs involving *S. intermedia* or *H. scutatum*.

I collected tissue samples from 271 individuals and found seven different biotypes of unisexual salamanders at 37 sites, and as many as four different biotypes at a single site (Table 4). Unisexual salamanders coexisted with *A. texanum* at 16 sites, *A. tigrinum* at 15 sites, *A. laterale* at 10 sites, and *A. jeffersonianum* at 9 sites. I found that unisexual salamanders coexisted with two or more species 46% of the time and were the most common pond-breeding salamander at 68% of their sites.
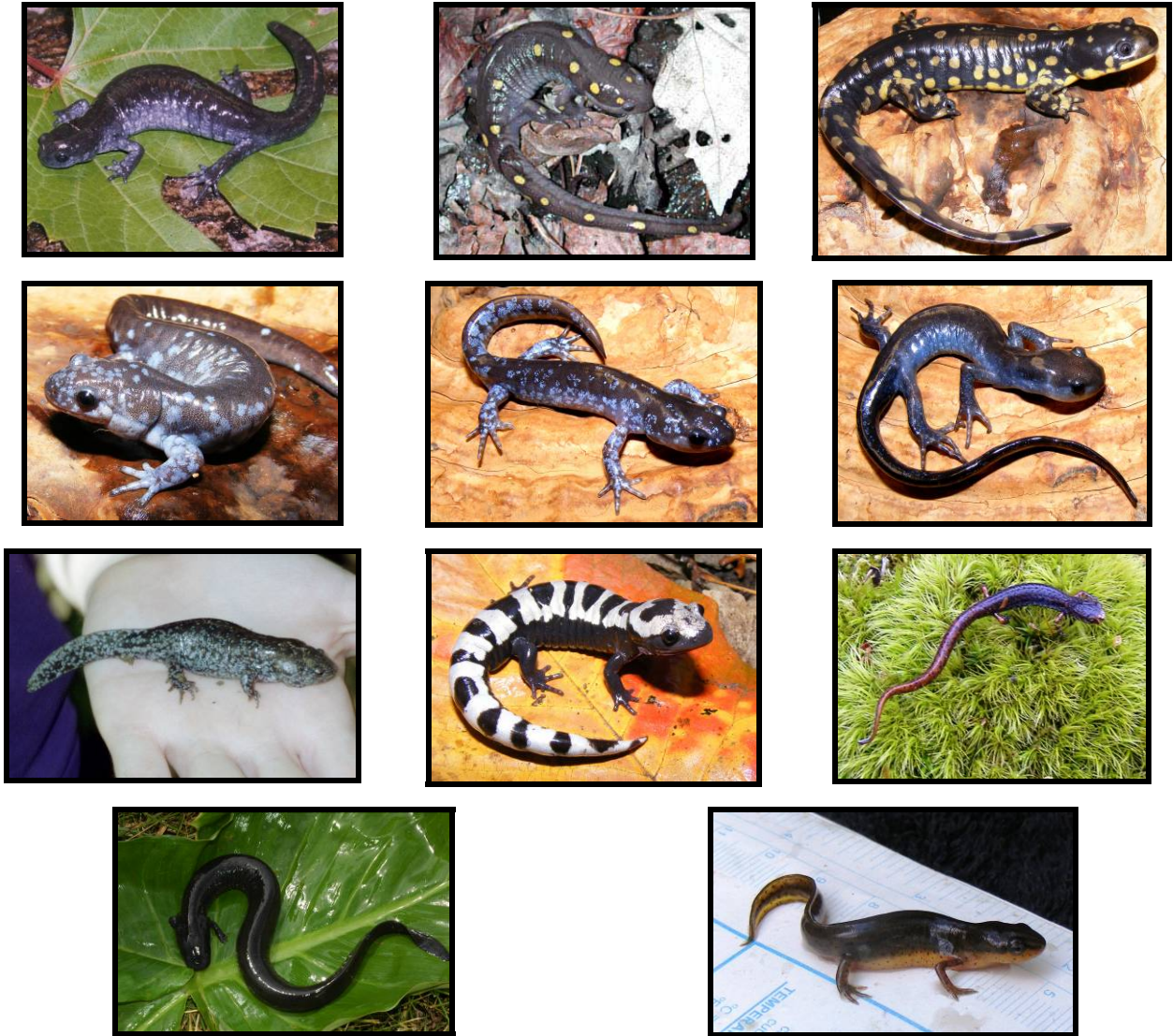
FIGURE 2. Pond-Breeding salamanders observed while conducting surveys in Ohio, Indiana, Illinois and Michigan, USA. The species are: top row (left to right) *Ambystoma texanum, A. maculatum,* and *A. tigrinum*; second row (left to right) unisexual *Ambystoma, A. laterale,* and *A. jeffersonianum*; third row (left to right) *A. talpoideum, A. opacum,* and *H. scutatum*; bottom row (left to right) *S. intermedia,* and *N. viridescens*. (Photos by Robert Brodman).

TABLE 2. Pond-breeding salamander assemblages from surveys conducted in Ohio, Indiana, Illinois, and Michigan, USA. The number at the top of each column indicates the number of sites that the species was present without any coexisting species. The remaining values are the number sites that the species coexisted with each corresponding species.

	atg	atx	atl	aj	us	al	am	ao	nv	hs	si
A. tigrinum (atg)	38										
A. texanum (atx)	15	26									
A. talpoideum (atl)	0	1	0								
A. jeffersonianum (aj)	3	6	0	3							
unisexuals (us)	15	16	1	9	0						
A. laterale (al)	35	5	0	0	9	10					
A. maculatum (am)	7	11	1	2	4	8	5				
A. opacum (ao)	4	10	2	3	3	0	6	5			
N. viridescens (nv)	18	1	0	2	2	13	5	4	1		
H. scutatum (hs)	1	2	0	0	0	3	0	0	0	0	
S. intermedia (si)	6	3	0	0	0	5	2	2	1	0	3

TABLE 3. Significant salamander community associations revealed by regression models from surveys conducted in Ohio, Indiana, Illinois, and Michigan, USA. The abundance of salamanders (dependent variable) is explained by the abundance of predictor species. Values are regression coefficients (*r*), degrees of freedom (df), *F* statistic, and *P*-values. The relationship between species is indicated as positive (+) or negative (-).

Dependent variable	Predictors	*r*	df	*F*	*P*
A. tigrinum	*A. texanum* (-), *A. jeffersonianum* (-), *A. maculatum* (-), *N. viridescens* (+)	0.361	4,178	6.54	< 0.001
A. texanum	*A. tigrinum* (-), *A. laterale* (-), *N. viridescens* (-)	0.395	3,178	16.24	< 0.001
A. laterale	*A. texanum* (-), *A. jeffersonianum* (-), *N. viridescens* (+)	0.415	3,178	12.17	< 0.001
A. jeffersonianum	Unisexuals (+), *A. opacum* (+)	0.461	2,178	23.77	< 0.001
Unisexuals	*A. jeffersonianum* (+)	0.347	1,178	24.21	< 0.001
A. maculatum	*A. tigrinum* (-), *N. viridescens* (+)	0.259	2,178	6.21	0.002
A. opacum	*A. jeffersonianum* (+), *A. talpoideum* (+), *N. viridescens* (+)	0.536	3,178	23.52	< 0.001
A. talpoideum	*A. opacum* (+), *A. texanum* (+)	0.401	2,178	16.89	< 0.001
N. viridescens	*A. tigrinum* (+), *A. texanum* (+), *A laterale* (+), *A. maculatum* (+), *A. opacum* (+)	0.399	5,178	8.25	< 0.001

TABLE 4. Unisexual salamanders and coexisting sexual species. Data are location of sites, biotype of unisexual salamanders based on nuclear chromosomes, and coexisting species. The Unisexual biotype column below designates the ploidy type by the first letter of its species epithet (i.e. JJ is a diploid *Ambystoma jeffersonianum* and LJT is a triploid hybrid with *A. laterale*, *A. jeffersonianum*, and *A. texanum* complements of chromosomes) where: L = *A. laterale*, J = *A. jeffersonianum*, T = *A. texanum*, and Ti = *A. tigrinum*.

Location	Unisexual biotype	Coexisting species
Adams Co., IN, site 1	LJT, LLJ	*A. texanum*
Adams Co., IN, site 2	LJT, LLJ	*A. texanum*
Franklin Co., IN, site 1	LJJ	*A. jeffersonianum*
Franklin Co., IN, site 2	LJJ	*A. jeffersonianum*
Franklin Co., IN, site 3	LJJ	*A. jeffersonianum*
Franklin Co., IN, site 4	LJJ, LJJJ	*A. jeffersonianum*
Huntington Co., IN, site 1	LJJ	*A. texanum, A. tigrinum*
Huntington Co., IN, site 2	LJT	*A. texanum*
Jay Co., IN, site 1	LJJ	*A. texanum, A. tigrinum*
Jay Co., IN, site 2	LJJ, LJT	*A. laterale, A. texanum*
Jennings Co., IN	LJJ	*A. jeffersonianum, A. texanum*
LaGrange Co., IN	LLJ	*A. laterale*
Martin Co., IN	LLJ	*A. jeffersonianum, A. texanum*
Owens Co., IN	LJJ	*A. jeffersonianum, A. opacum, A. tigrinum*
Posey Co., IN	LJT	*A. maculatum, A. opacum, A. talpoideum, A. texanum*
Pulaski Co., IN, site 1	LJJ	*A. tigrinum*
Pulaski Co., IN, site 2	LLJ	*A. laterale, A. maculatum, A. tigrinum*
Pulaski Co., IN, site 3	LLJ	*A. laterale*
Pulaski Co., IN, site 4	LLJ	*A. laterale*
Pulaski Co., IN, site 5	LLJ	*A. laterale*
Saint Joseph's Co., IN	LJJ	*A. laterale, A. tigrinum, N. viridescens*
Steuben Co., IN, site 1	LLJ	*A. laterale, A. tigrinum*
Steuben Co., IN, site 2	LLJ	*A. laterale*
Steuben Co., IN, site 3	LLJ	*A. laterale*
Wabash Co., IN, site 1	LJJ, LJJJ, LJJTi, LJTi	*A. tigrinum*
Wabash Co., IN, site 2	LJJ	*A. tigrinum*
Wabash Co., IN, site 3	LJJ	*A. tigrinum*
Wabash Co., IN, site 4	LJJ	*A. texanum, A. tigrinum*
Wabash Co., IN, site 5	LJJ	*A. texanum, A. tigrinum*
Wabash Co., IN, site 6	LJJ, LJJJ	*A. texanum, A. tigrinum*
Wabash Co., IN, site 7	LJJ	*A. texanum*
Wabash Co., IN, site 8	LJJ, LJT	*A. texanum*
Wabash Co., IN, site 9	LJJ, LJT	*A. texanum*
Wells, Co., IN	LJJ, LJT, LT	*A. jeffersonianum, A. texanum, A. tigrinum*
Cuyahoga Co., OH, site 1	LJJ	*A. jeffersonianum, A. maculatum*
Cuyahoga Co., OH, site 2	LJJ	*A. jeffersonianum, A. maculatum, N. viridescens*
Ottawa Co., OH	LJT, LJTi	*A. opacum, A. texanum, A. tigrinum*

TABLE 5. Post-hoc results for effects of wetland cluster size on pond-breeding salamander communities. Variables are the number of wetlands in a wetland cluster, mean salamander species richness, mean community abundance, and percent occupancy. Subsets that are significantly different (Tukey HSD, post-hoc test, α = 0.05) are indicated with different superscripts. *F* statistic with degrees of freedom and *P*-values from MANOVA are shown.

Wetland Cluster	Richness	Abundance	Occupancy
14 or more	2.3[a]	5.0[a]	46.5[a]
2-13	1.8[b]	4.7[a]	29.8[b]
1 (isolated)	1.1[c]	1.9[b]	20.0[c]
$F_{2, 202}$	3.69	3.34	10.00
P	0.027	0.038	< 0.001

LJJ (triploid hybrid with one chromosome set from *A. laterale* and two sets from *A. jeffersonianum*) was the most common unisexual biotype, found at 62% of the unisexual sites, and they most frequently coexisted with *A. texanum, A. tigrinum,* and *A. jeffersonianum.* LLJ occurred at 30% of the unisexual sites and most frequently coexisted with *A. laterale.* LJT occurred at 24% of the unisexual sites and most frequently coexisted with *A. texanum.* The remaining unisexual biotypes were uncommon and only found at sites that also had LLJ, LJJ, or LJT. Two or more unisexual biotypes coexisted at 27% of the unisexual sites and most of these sites were found in the Upper Wabash watershed in northeastern Indiana. Unisexual populations that had *A. texanum* chromosomes (LJT, LT) or *A. tigrinum* chromosomes (LJTi, LJJTi) where significantly more likely to coexist with *A. tigrinum* or *A. texanum* than *A. laterale* or *A. jeffersonianum* ($\chi^2 = 16.45$, df = 7, $P = 0.021$). Unisexual populations with mostly *A. jeffersonianum* chromosomes (LJJ, LJJJ) where significantly more likely to coexist with *A. jeffersonianum* than *A. laterale,* and unisexual populations with mostly *A. laterale* chromosomes (LLJ) were significantly more likely to coexist with *A. laterale* than *A. jeffersonianum* ($\chi^2 = 10.57$, df = 7, $P = 0.014$).

Landscape variables.—The number of wetlands within wetland clusters significantly affected species richness, abundance, and occupancy of pond-breeding salamanders. Wetland clusters of 14 or more wetlands had significantly greater, and isolated wetlands had significantly less, species richness and percentage occupancy than wetland clusters with 2–13 wetlands (Table 5). Isolated wetlands had significantly lower salamander abundance than sites with two or more wetlands. The number of hydroperiod classes within a wetland cluster significantly affected species richness, abundance, and occupancy of pond-breeding salamanders. Sites with all three hydroperiod classes had significantly greater species richness, abundance, and occupancy of salamanders than sites with two hydroperiod classes, and sites with one hydroperiod class had significantly lower abundance and occupancy than sites with two hydroperiod classes (Table 6). Sites with 14 or more wetlands had significantly more *A. texanum* than isolated sites ($F_{2, 63} = 5.78$; $P = 0.02$), and sites with all three hydroperiod classes had significantly more *A. texanum* than sites with one or two hydroperiod classes ($F_{2, 63} = 3.14$; $P = 0.05$). There was a significant interactive effect of number of wetlands and hydroperiod classes on *A. maculatum* abundance with them being more abundant at sites with greater number of wetlands and hydroperiod classes ($F_{1, 130} = 6.02$, $P = 0.016$).

Population trends.—Of the 136 populations that I monitored at the 47 long-term sites, 84% of the populations were stable fluctuations, 11% increased, and 6% decreased (Table 7). Most of the populations with significant population trends were from Tefft Savanna Nature Preserve and Jasper-Pulaski Fish and Wildlife Area in northwest Indiana, and most of these trends were increases. Although *A. maculatum* had no significant trends at any of the sites, there was a significant decrease over time when I pooled all sites.

TABLE 6. Post-hoc results for hydroperiod effects on pond-breeding salamander communities. Variables are the number of hydroperiod classes, mean amphibian species richness, mean community abundance, and percent occupancy. Subsets that are significantly different (Tukey HSD, post-hoc test, α = 0.05) are indicated with different superscripts. *F* statistic with degrees of freedom and *P*-values from MANOVA are shown.

Hydroperiod	Richness	Abundance	*Occupancy.*
3	2.3[a]	5.6[a]	42.8[a]
2	1.8[b]	4.3[b]	32.8[b]
1	1.3[b]	2.5[c]	21.6[c]
$F_{2,202}$	3.90	4.79	4.47
P	0.022	0.009	0.013

TABLE 7. Significant population trends of pond-breeding salamanders. Variables are number of years that the population was monitored, Kendall's *tau* correlation coefficients, and *P*-values.

Species	Location	Time (years)	*tau*	*P*
A. tigrinum	Saint Joseph's College, Jasper Co., IN	7	0.707	0.050
	Tefft Savanna pond 9, Jasper Co., IN	15	0.597	0.005
	Tefft Savanna pond 10, Jasper Co., IN	15	0.584	0.006
	Jasper-Pulaski pond 25, Jasper Co., IN	15	0.525	0.015
	Shepherd's Swamp, Jasper Co, IN	7	-0.853	0.015
A. texanum	Koontz Lake, Starke Co., IN	8	-0.775	0.039
A. laterale	Jasper-Pulaski pond 24, Jasper Co., IN	15	0.525	0.022
	Jasper-Pulaski pond 69, Pulaski Co., IN	15	-0.690	0.050
	Koontz Lake, Starke Co., IN	8	-0.800	0.009
A. opacum	Twin Swam, Posey Co., IN	9	0.719	0.001
	Glendale, Davies Co., IN	9	0.589	0.005
	Minnehaha, Greene Co., IN	9	0.505	0.021
	Sandusky, OH	7	0.429	0.043
A. jeffersonianum	Morgan-Monroe State Forest, Monroe Co., IN	12	-0.648	0.045
A. maculatum	Pooled from all sites	19	-0.471	0.046
Unisexuals	Salamonie State Forest, Wabash Co., IN	10	-0.619	0.048
N. viridescens	Tefft Savanna pond 9, Jasper Co., IN	15	0.553	0.010
	Tefft Savanna pond 10, Jasper Co., IN	15	0.488	0.004
	Jasper-Pulaski pond 24, Jasper Co., IN	15	0.544	0.018
	Jasper-Pulaski pond 25, Jasper Co., IN	15	0.537	0.011
	Jasper-Pulaski pond 38, Jasper Co., IN	15	0.522	0.015
H. scutatum	Koontz Lake, Starke Co., IN	8	-0.567	0.050
S. intermedia	Jasper-Pulaski pond 56, Pulaski Co., IN	15	0.497	0.021
	Jasper-Pulaksi pond 62, Pulaski Co., IN	15	-0.738	0.047

No other species had a significant trend from pooled data. Detectability of populations among years ranged from 77 to 81%.

Springtime prescribed burns.—Just over half of the long-term sites experienced one or two springtime prescribed burns while I monitored salamander

TABLE 8. The effect of springtime prescribed burns on pond breeding salamanders. The values are degrees of freedom (df), *F* statistic, and *P*-values from ANOVA. All significant results are declines.

Species	df	*F*	*P*
A. texanum	1,116	4.35	0.039
A. tigrinum	1,273	7.24	0.008
N. viridescens	1,232	13.13	< 0.001
S. intermedia	1,99	2,12	0.149
H. scutatum	1,10	18.99	0.002
A. maculatum	1,124	14.07	< 0.001
A. laterale	1,214	120.7	< 0.001
A. jeffersonianum	1,71	25.43	< 0.001
Unisexuals	1,85	10.82	0.001
A. opacum	1,74	7.99	0.006

populations. I excluded *A. talpoideum* from this analysis because none of the sites where I found this species had prescribed burns. Spring burns had a significant effect on the abundance of nine species of pond breeding salamanders (Table 8). MANOVA detected a significant interactive effect of spring burns and hydroperiod classes on salamander abundance with salamanders being less abundant at burn sites with less than three hydroperiod classes ($F_{1, 9} = 4.186$, $P = 0.046$). I also observed large increases of *A. tigrinum* and *N. viridescens* at two sites during the spring after a fall burn. Declines were not associated with fall or winter burns. Species declined in abundance from 25–100% in the year following the burn (Fig. 3), although the decrease in the fully aquatic *S. intermedia* was not significant due to high variance. The six forest species were the most affected and experienced greater than 80% declines following a spring burn. The forest species took a mean of 4.6 years to recover to pre-burn levels. Prescribed spring burns also negatively affected the species that use open habitats, *A. tigrinum, A. texanum,* and *N. viridescens*; however, their mean time to recover was just 1.6 years and often exceeded pre-burn abundance. The forest species took significantly more time for populations to
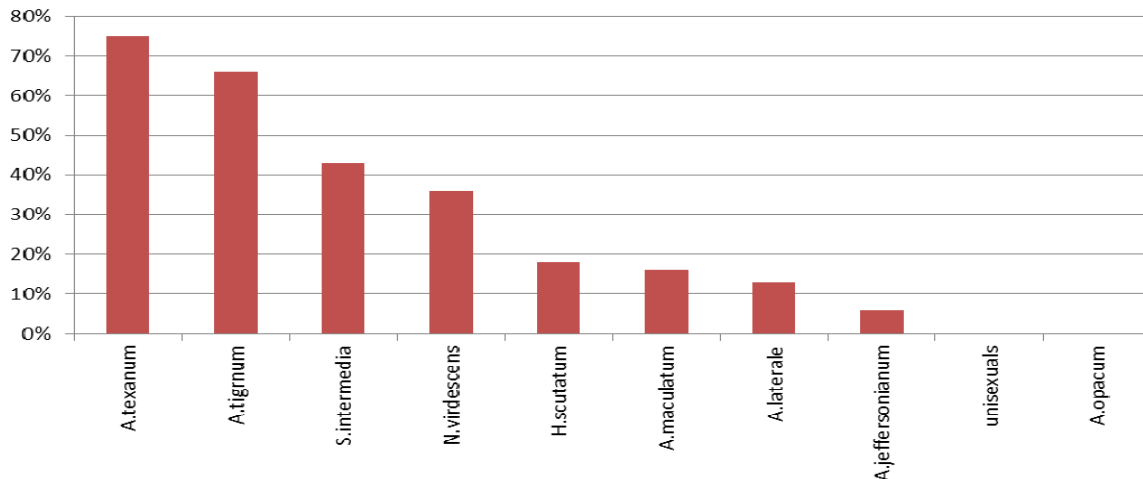
FIGURE 3. The mean abundance of pond-breeding salamander the year after springtime prescribed burns relative to pre-burn abundance.

recover post-burn than the open habitat species ($F_{1, 44} = 84.91$, $P < 0.001$).

DISCUSSION

Salamander surveys.—The two most common species, *A. tigrinum* and *A. texanum,* are generalists with regard to adult and juvenile habitat using both forest and open habitats, such as savannas and grasslands (Bishop 1943; Pfingsten and Downs 1989; Minton 2001). *Siren intermedia* and *N. viridescens* are primarily aquatic and use semi-permanent to permanent wetlands and ponds with fish (Bishop 1943; Pfingsten and Downs 1989; Minton 2001). The remaining species require mature, preferably deciduous, forested uplands as adult and juvenile habitat, and fishless seasonal wetlands for breeding (Bishop 1943; Pfingsten and Downs 1989; Minton 2001).

Community associations.—Unisexual salamanders, *N. viridescens*, *A. maculatum, A. laterale,* and *A. tigrinum* were the best indicators of pond-breeding salamander abundance and diversity. In previous studies, *Ambystoma laterale* was an indicator of amphibian and reptile diversity and the quality of oak savanna habitat (Brodman et al. 2005; Brodman 2009b). *Ambystoma tigrinum* and *A. texanum* were two of the most commonly encountered species, and other species infrequently coexisted with either *A. tigrinum* or *A. texanum*. The fact that both species are the most generalist in habitat requirements (Bishop 1943; Pfingsten and Downs 1989; Minton 2001) suggests that they may be better competitors in marginal habitats.

The larval assemblages of pond-breeding salamanders are often under intense competition and intraguild predation (Wilbur 1972; Fauth and Resetarits 1991; Brodman 1996; Hairston 1996; Jaskula and Brodman

2000; Brodman 2004; Brodman and Krouse 2007). However, I observed more breeding sites with four or more species coexisting than expected. This suggests that niche partitioning (Brodman 1996) or keystone interactions (Fauth and Resetarits 1991; Brodman 2004) may facilitate coexistence.

Unisexual salamanders must coexist with *A. laterale, A. jeffersonianum, A. texanum,* or *A. tigrinum* to carry out their unique mode of reproduction (Bogart et al. 2007; Bi et al. 2008). Female unisexuals usually reproduce by gynogenesis with unreduced eggs and sperm from coexisting males required to activate the eggs without fertilization (Bogart et al. 2007; Bi et al. 2008). However, unisexuals also reproduce by kleptogenesis where they "steal" chromosomes from sympatric sexual species to elevate the ploidy or to replace one of the nuclear genomes of their offspring (Bogart et al. 2007; Bi et al. 2008). This results in a variety of at least 20 different genomic biotypes involving chromosomes of four sexual species. I report 10 of the unisexual biotypes coexisting with all four sexual bisexual species in my study area. I found an association between the biotype of unisexuals and their coexisting sexual species. LLJ unisexual biotypes were associated with *A. laterale*, LJJ and LJJJ unisexual biotypes were associated with *A. jeffersonianum*, and LLT, LJT, LT, LJJT, LJTTi, LJTi, and LJJTi unisexual biotypes were associated with *A. texanum* and *A. tigrinum*. This pattern is consistent with ploidy elevation and genome replacement and supports the hypothesis of kleptogenesis as a reproductive mode for unisexual salamanders.

Landscape variables.—I found that pond-breeding salamanders were widespread but fragmented by development and agriculture. This study provides

further data in support of the hypothesis that the density of wetlands in the landscape and hydroperiod heterogeneity influences amphibian abundance, occupancy, and diversity (Brodman and Kilmurry 1998; Lannoo 1998; Naugle et al. 2005; Price et al. 2005; Brodman 2009b).   This study also provides further support for the hypothesis that ephemeral and seasonal wetlands are ecologically important for the conservation of salamanders because of their unique assemblages of species, roles in habitat connectivity, and recruitment of juveniles during years that are wetter than average (Lannoo 1998; Semlitsch 1998; Semlitsch and Bodie 1998; Snodgrass et al. 2000; Egan and Paton 2004). The primary land management recommendation for the conservation of pond-breeding salamander diversity is protecting a 200–250 m buffer of mature deciduous forest around vernal ponds (Semlitsch 1998; Porej et al. 2004; Rubbo and Kiesecker 2005). Breeding sites need to be part of wetland complexes that encompass hydroperiod heterogeneity (Lannoo 1998; Snodgrass et al. 2000; Petranka et al. 2004; Brodman 2009b) and connectivity for dispersal (Rothermel 2004; Rubbo and Kiesecker 2005; Rittenhouse and Semlitsch 2006; Compton et al. 2007; Petranka et al. 2007). Wetland clusters need to be considered as land management units for the conservation of pond-breeding salamanders (Petranka et al. 2004).

Population trends.—I observed fluctuations of pond-breeding salamanders at long-term monitoring sites, but populations were generally stable during this study. I estimated that detectability of pond-breeding salamanders in this study was generally high. This corroborates a five year study on four species of pond-breeding salamanders at 32 ponds where detectability ranged from 76–98% (Church 2008). Annual variation in climate explains most of amphibian population fluctuations in many populations (Hairston 1996; Brodman 2002; Petranka et al. 2003; Blackwell et al. 2004; Petranka et al. 2007; Brodman 2009b). Some exceptions include populations impacted by human land use, and the decline of *A. jeffersonianum* at Morgan-Monroe that was associated with an outbreak of the chytrid fungus *Batrachochytrium dendrobatidis* (Brodman and Briggler 2008). The Morgan-Monroe population started to recover in 2009. Forest species such as *A. laterale* and *A. maculatum* have also declined in Illinois (Grant 1936; Smith 1961; Mierzwa 1998), elsewhere in Indiana (Minton 2001; Brodman 2005), and throughout their ranges where native forests and wetlands have been replaced by agriculture and development (Petranka 1998). Fire management to open oak savanna canopy and competition with *A. tigrinum* and unisexual populations could be factors in some declines (Jaskula and Brodman 2000; Brodman and Krouse 2007).

Springtime prescribed burns.—Prescribed burning is an important management tool to promote plant diversity in suppressed habitats and to control invasive species (Abrams 1992).   However, most pond-breeding salamanders in the northeast and Midwest regions of USA are associated with wetlands within forested areas (Minton 2001; Guerry and Hunter 2002) and I have often observed burning during the spring breeding migration. Most studies have found that prescribed burns cause little direct mortality to amphibians and reptiles (McLeod and Gates 1998; Moseley et al., 2003; Keyser et al. 2004). However, studies investigating the impact of fire on amphibians and reptiles tend to focus more on reptiles than amphibians, more on anurans than salamanders, and more on terrestrial-breeding salamanders than on pond-breeding salamanders (McLeod and Gates 1998; Moseley et al., 2003; Pilliod et al. 2003; Dechant 2007). Conclusions are usually restricted to the most abundant species encountered, and often there are too few pond-breeding salamanders sampled to analyze trends. A second problem is that if the study only focuses on use of a habitat, then changes in abundance can be explained by two alternate hypotheses. The change in relative abundance may reflect a real change in population size due to changes in mortality or birth rates, or the change in relative abundance may be caused by changes in behavior that affect detectability. The advantage of focusing on the abundance of breeding adults, eggs, and larvae at a breeding site is that changes in birth rates can be detected regardless of whether they are due to mortality or behavioral changes.

The Global Amphibian Assessment concluded that forest habitats have the highest proportion of threatened amphibian species and that fire is the third greatest threat to amphibians (IUCN et al. 2008). I found short-term declines of pond-breeding salamanders after springtime prescribed burns. Elsewhere salamanders have been shown to be less abundant on burn sites than on control forest sites (McLeod and Gates 1998). Although most populations were observed to recover in five years or less, it is possible that if sites were burned more frequently than once a decade, then the populations may not be able to recover. In a long-leaf pine community, it takes more than two years for salamanders to return to burn sites and this suggests that burning should be no more frequent than once every 3–7 years (Schurbon and Fauth 2003).   The period of population recovery is similar to the time that it takes ambystomatid salamander populations to recover from the negative impact of clear-cutting forest habitat (Raymond and Hardy 1991; DeMaynadier and Hunter 1999; Renken et al. 2004; Morris and Maret 2008).

Long-term studies of metacommunities and metapopulations are valuable to ecological modeling and conservation designs (Cody 1996; Storfer 2003; Daszak

et al. 2005; Whiteman and Wissinger 2005; Milne and Bennett 2007). We need a better understanding of the dispersal ecology of pond-breeding salamanders and landscape factors that might impede the colonization of salamanders to new breeding sites. Additional research needs to focus on long-term responses of metapopulations to prescribed burns, and management of invasive plants. We need to design adaptive management protocols that incorporate the natural and life history of pond-breeding salamanders. Examples include implementing buffers to core habitat, firebreaks to create refuges, and timetables that work around salamander activity.

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BOB BRODMAN is a Professor of Biology and Environmental Science, and Chair of the Biology Department at Saint Joseph's College in Indiana where he teaches a variety of Biology, Zoology and Ecology classes, and commands an army of undergraduate students in amphibian population research. He is pictured here with a Lesser Siren (*Siren intemedia*) in a minnow trap. He received his Ph.D. in Ecology from Kent State University working under Dr. Lowell P. Orr. This study is a product of his two-decade long obsession with *Ambystoma* and other pond-breeding salamanders. He is currently on the advisory board for Midwest Partners for the Conservation of Amphibians and Reptiles, Chair of a technical advisory committee on herps for the Indiana Department of Natural Resources, and was co-organized the first ever *Herpetological Conservation & Biology* Symposium for the 6th World Congress of Herpetology in Brazil (August 2008).