
A 14-YEAR STUDY OF AMPHIBIAN POPULATIONS AND METACOMMUNITIES

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Abstract.—I used data from a 14 year survey of the amphibian fauna (14 species) in Jasper County, Indiana, USA, to detect population and diversity trends, and to test hypotheses regarding the influence of landscape, climatic, and biotic factors on amphibian abundance, occupancy, and diversity. Suitable amphibian habitats throughout the county were sampled by a combination of anuran call indices, density estimates, and per effort catch. The number of amphibian breeding sites, total amphibian abundance, and demographics of five species increased over time, while species richness/site, and mean breeding index of eight species decreased. The abundance of two species, Spring Peepers (*Pseudacris crucifer*) and Eastern Gray Treefrogs (*Hyla versicolor*), were the best indicators of overall amphibian biodiversity. Most species were associated with one or two other species. Demographics of most species were influenced by at least one climatic variable, and for most species, climatic variation among years was more important than time in explaining amphibian population trends. Winter and spring precipitation, as well as fall, winter, and spring temperatures, were the most important climatic variables influencing the abundance, occupancy, and diversity of amphibians in Jasper County. Amphibian demography and landscape data supported the hypothesis that the degree of wetland isolation and hydroperiod heterogeneity influence amphibian abundance, occupancy, and diversity. The number of wetlands in a cluster and the number of hydroperiod classes explained geographic variation in amphibian abundance, occupancy, and diversity. At the landscape level, large amphibian metacommunities were associated with large wetland clusters, hydroperiod heterogeneity, and high conservation priority upland habitats.

Key Words.—amphibians; long-term monitoring; population trends; metacommunities; metapopulations

INTRODUCTION

Long-term field studies are valuable to ecologists and conservation efforts for several reasons. They increase the possibility of discovering rare events and the results of slow processes (Diamond 1996; Whiteman and Wissinger 2005). They are important for identifying factors, such as climate and habitat variables, that affect population dynamics and community structure (Cody 1996; Daszak et al. 2005; Whiteman and Wissinger 2005). They also provide base-line data and continued monitoring for environmental management (Spellerberg 1991; Cody 1996). There has been much attention to metapopulation (Hastings and Wolin 1989) and metacommunity (Wilson 1992) models for use in ecology and conservation (Levin 1992; Cody 1996; MacKenzie et al. 2002). Conservation efforts need research at the landscape level that focuses on the ecological value of nature preserves (Storfer 2003; Milne and Bennett 2007). However, few long-term studies of amphibians have focused on entire communities at large scales. Long-term monitoring of amphibians tends to focus on one to several breeding sites. Temporal scales integrated within spatial scales are lacking (Cody 1996).

Meta-analysis of more than 200 studies on amphibian populations indicates that there has been a worldwide decline during the last four decades for unknown reasons

(Houlahan et al. 2000; Alford et al. 2001; Stuart et al. 2004). However, only a few of the studies used in these analyses spanned more than 10 consecutive years, or involved two or more interacting species (Hairston 1996; Gibbons et al. 1997; Sexton et al. 1998). Some long-term studies are on one or a few pond-breeding amphibian species at a single site (Hairston 1996; Semlitsch et al. 1996; Sexton et al. 1998; Petranka et al. 2004; Whiteman and Wissinger 2005). Others are a repeat of short-term (1–3 year) inventories after an interval without monitoring populations (Lannoo et al. 1994; Skelly et al. 1999; Brodman et al. 2002; Seigel et al. 2002; Woinarski et al. 2006) or are just a few years in duration (Brodman et al. 2006; Pieterse et al. 2006). Others rely on one demographic measure such as egg mass density (Brodman 2002), larval sampling (Cortwright 1998), or frog calls (Mossman et al. 1998; deSolla et al. 2005, 2006; Pieterse et al. 2006). 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). Therefore, studies need to be at least 7–10 consecutive years to detect biologically meaningful trends of amphibian populations and to examine the importance of abiotic and biotic factors that affect population dynamics and community structure (Sexton



FIGURE 1. Map of Indiana showing the location of Jasper County in grey. The location of Indiana is indicated in the inset map of the USA.

et al. 1998; Pechmann pers. comm.). Wetland clusters, rather than individual ponds, should be the monitoring units of long-term studies on pond-breeding amphibians (Petranka et al. 2004). Sampling of certain species and assemblages of species in a landscape context requires multiple methods (Brodman 2003). However, few continuous long-term studies of metacommunities at the landscape scale exist.

Lannoo (1998) hypothesized that pond-breeding amphibians would do best in a landscape composed of wetlands with varying hydrology. One reason is that sink and source populations within a metapopulation fluctuate among years because climate affects wetland quality and quantity (Lannoo 1998). For example, if amphibians could migrate wetland to wetland, then during a year of normal weather, source populations should be those that breed in fish-free semi-permanent and seasonal wetlands. Seasonal wetlands could transform into ecological sinks during unusually dry years if they dried before resident amphibians completed metamorphosis. Permanent wetlands would typically serve as ecological sinks because they harbor larger predators such as fish, herons, and water snakes. Although ephemeral wetlands lack most predators, they would be ecological sinks if their hydroperiod is too short for larval development and metamorphosis. However, during wetter than average years, ephemeral and seasonal wetlands become the best source habitats, because amphibian larval development ensues in the relative absence of predators. During severe droughts, when semi-permanent wetlands dry, or following a

winter kill, the permanent wetlands form refuges for amphibians and become source habitats. A second reason is that within a metapopulation the sink habitats can function as corridors between distant source populations (MacArthur and Wilson 1967; Semlitsch and Bodie 1998; Naugle et al. 2005). The Lannoo model predicts that amphibian abundance, occupancy, and species richness is highest in large wetland clusters with a variety of ephemeral, seasonal, semi-permanent, and permanent wetlands, and lower in isolated wetlands and small clusters lacking variation in hydroperiod (Semlitsch and Bodie 1998).

Climate change is one possible direct or indirect cause of amphibian declines (Alexander and Eischeid 2001; Kiesecker et al. 2001; Pounds et al. 2006). We need long-term studies on large scales to determine how climate perturbations contribute to long-term population dynamics. Such data may predict amphibian trends in a changing climate. I expect that amphibians would do best in years with wet springs after wet falls and mild winters and do poorest in years with harsh winters and droughts.

Here, I report population and community trends of 14 species of pond-breeding amphibians during a 14-year countywide survey. The objectives of this study are to: (1) detect trends in amphibian abundance and diversity over time, and to test the hypothesis of recent amphibian declines; (2) determine biotic associations among amphibian species; (3) model climatic variables as a potential explanation of variation in amphibian abundance, occupancy, and diversity, and to discuss potential impacts of climate change; (4) model the roles of hydroperiod heterogeneity, and the degree of clustering and isolation among potential breeding sites as factors explaining amphibian abundance, occupancy, and diversity, and to test the Lannoo Model that amphibians do best in larger wetlands clusters with varying hydrology; and (5) determine landscape factors associated with large amphibian metacommunities. Because of the size of the study area and duration of the study, these data will fill an important gap in our understanding of amphibian population and community dynamics.

MATERIALS AND METHOD

We identified all potential amphibian breeding sites with wetland inventory maps and field observations of Jasper County (1450 km²), in northwest Indiana, USA (Fig. 1). Pre-settlement habitat was a mosaic of grassland, oak savanna, and vast wetland complexes; however, by the early 20th century widespread conversion of these to row crops (corn and soy) prevailed (Lindsey et al. 1969). Remnant natural habitats include patches of oak savanna, woodlots, grasslands, wetlands, and vegetated riparian zones. I

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TABLE 1. Number of amphibian populations, breeding sites, and mean number of species per site in Jasper County, Indiana, USA from 1994–2007. Kendall's Tau revealed trends ($^{\circ}0.05 > P < 0.1$) and significant correlations ($^bP < 0.05$, $^cP < 0.01$, $^dP < 0.001$).

	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	Mean	Tau
<i>Pseudacris crucifer</i>	164	94	105	225	383	201	223	219	303	270	205	210	170	233	214.6	ns
<i>Pseudacris triseriata</i>	142	91	88	147	288	213	176	150	235	213	123	177	102	154	164.2	ns
<i>Hyla versicolor</i>	120	18	73	93	188	114	7	100	99	272	263	78	51	50	109.0	ns
<i>H. chrysoscelis</i>	24	7	19	23	17	9	50	18	8	42	27	23	2	22	20.8	ns
<i>Acris blanchardi</i>	0	0	0	0	0	2	4	6	11	19	28	5	6	17	7.0	0.73 ^d
<i>Bufo americanus</i>	89	40	25	64	179	131	29	101	178	231	68	81	137	189	110.1	0.36 ^b
<i>Bufo fowleri</i>	45	15	42	47	83	47	84	68	46	136	183	58	38	40	66.6	0.29 ^a
<i>Rana pipiens</i>	23	20	9	15	16	21	17	34	25	37	38	17	41	35	24.9	0.51 ^c
<i>R. clamitans</i>	57	21	52	44	44	40	45	106	64	147	143	75	37	46	65.8	ns
<i>R. catesbeiana</i>	21	13	20	13	17	16	30	14	16	27	27	22	6	13	18.2	ns
<i>Ambystoma laterale</i>	7	8	8	4	6	6	2	2	1	5	6	6	5	8	5.3	ns
<i>A. tigrinum</i>	9	8	5	6	4	2	3	5	3	3	13	8	8	13	6.4	ns
<i>Notophthalmus viridescens</i>	0	0	3	2	1	5	1	3	1	1	5	2	5	4	2.4	0.41 ^b
<i>Siren intermedia</i>	0	0	1	1	2	1	0	2	1	2	3	4	2	3	1.6	0.67 ^c
Anura	685	319	433	671	1215	794	665	816	985	1395	1105	746	590	800	801.4	0.30 ^a
Caudata	16	16	17	13	13	14	6	12	6	11	27	20	20	28	15.6	0.30 ^a
Populations	701	335	450	684	1228	808	671	828	991	1406	1132	766	610	828	817.0	ns
Sites	237	124	173	312	520	371	304	371	439	509	466	378	244	304	339.4	0.28 ^a
Species/site	3	2.7	2.6	2.2	2.4	2.2	2.2	2.2	2.3	2.8	2.4	2.0	2.5	2.7	2.4	ns

divided the county into 65 ha blocks, and conducted calling surveys from March–July for 14 consecutive years (1994–2007) in each block that contained one or more wetlands. Wetlands within a 65-ha block represented a single site. I surveyed a subset of wetlands from 60 sites each year for adult and larval salamanders, tadpoles, and eggs using visual searches, minnow traps, dipnets and seines. I quantified estimates of population abundance for each species at each site using a combination of anuran call indices, density estimates, and per effort catch. Detection is time-dependent (Crouch and Paton 2002; Pierce and Gutzwiller 2004; deSolla et al. 2005), so I visited each site once a month from March–July each year. I performed frog call surveys from 30 min to 4 h after sunset. I listened for frogs for 5 min at each site to identify the species that were present and to estimate population sizes using the Karns (1986) ordinal scale of breeding chorus intensity on scale of 0 to 5. Frog call intensity correlates well with egg mass density (Stevens and Paszkowski 2004). I categorized adult and larval salamanders, tadpoles, and egg mass abundance on an ordinal scale from 0 to 5 based on time constrained search-and-seize and catch per trap-day using minnow traps (Brodman 2003). I designated amphibian population abundance as the highest score from 0 to 5 obtained for a species at a sight during the sampling season. Species abundance in a given year was the sum of population sizes at all sites. Amphibian abundance at the community level was the sum of abundance indices from each species at each breeding site. I used species richness at sites and within metacommunities to measure amphibian diversity. Much of the field data collection included my students,

whom I trained and tested in class prior to conducting field work (see Brodman 2000a).

Occupancy measurements normally reflect the proportion of sites occupied by a species; however, occupancy models require estimates of detectability (MacKenzie et al. 2002). Survey design took place before the advent of occupancy models; thus, they do not meet the assumptions of the mathematical models. In my system, occupancy and detectability can change within the sampling season. This might occur if there is significant egg or hatchling mortality, if metamorphosis occurs before the sampling period for larvae and tadpoles takes place, or if certain life-history stages are more detectable than others. For example adult Blue-spotted Salamanders (*Ambystoma laterale*) are easier to find under logs than Tiger Salamanders (*A. tigrinum*), but the conspicuous Tiger Salamander egg masses are easier to detect than Blue-spotted Salamander eggs (Brodman, pers. obs.). Larvae of both species one-week post-hatching are difficult to detect; whereas, one-month old larvae are easiest to detect using dip-net, and two-month old larvae are easiest to detect using seines (Brodman, pers. obs.).

My protocol of sampling each month, with methods targeted to a certain life-history stage, is designed to greatly increase detectability of each species at a site. However, occupancy models do not assume that occupancy does not change between sampling seasons, or that detectability cannot change between sampling seasons do to climatic differences (MacKenzie et al. 2002). Thus, for the purpose of this study, occupancy is the percentage of years that I detected amphibians at a site.

TABLE 2. Mean population size (breeding index) of amphibians in Jasper County, Indiana, USA from 1994-2007. Kendal's Tau indicated trends (^a0.05 > P < 0.1) and significant correlations (^bP < 0.05, ^cP < 0.01, ^dP < 0.001) with year.

	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	Mean	Tau
<i>Pseudacris crucifer</i>	2.8	3.6	3.3	3.4	3.3	3.0	3.2	3.4	3.1	2.9	2.8	3.0	2.6	3.2	3.1	-0.35 ^b
<i>P. triseriata</i>	2.6	2.6	2.6	2.5	2.6	2.7	2.4	3.2	2.7	2.4	2.3	2.4	2.1	2.4	2.5	-0.35 ^b
<i>Hyla versicolor</i>	2.6	4.1	3.4	2.9	3.3	2.7	2.9	2.0	2.3	2.4	2.3	2.3	3.0	2.4	2.8	-0.46 ^b
<i>Hyla chrysoscelis</i>	2.0	3.0	2.4	2.5	2.4	2.0	2.1	1.8	2.1	1.9	2.0	2.3	2.0	2.2	2.2	-0.27 ^a
<i>Acris blanchardi</i>	0.0	0.0	0.0	0.0	0.0	2.5	1.5	2.3	2.3	2.4	3.3	2.2	2.0	1.7	1.4	0.42 ^b
<i>Bufo americanus</i>	2.2	2.2	2.2	2.5	2.5	2.5	2.1	2.2	2.9	2.4	2.2	2.6	2.6	2.7	2.4	0.42 ^b
<i>B. fowleri</i>	2.1	3.1	2.4	2.2	3.0	2.4	2.6	2.0	2.2	2.1	2.3	2.1	2.4	2.1	2.4	-0.32 ^a
<i>Rana pipiens</i>	1.8	1.7	1.4	1.5	1.9	1.8	1.4	1.7	2.0	1.7	2.0	1.2	2.4	1.7	1.7	-0.53 ^c
<i>R. clamitans</i>	2.2	2.7	2.3	2.5	2.3	2.2	1.6	1.9	2.0	2.1	2.1	1.7	2.1	1.6	2.1	-0.53 ^c
<i>R. catesbeiana</i>	2.0	2.2	2.3	1.9	1.8	1.6	1.7	1.4	1.5	1.8	1.7	1.5	1.8	1.5	1.8	-0.53 ^c
<i>Ambystoma laterale</i>	2.7	2.6	3.0	4.0	2.5	2.2	2.5	1.5	2.0	1.8	2.7	2.0	2.0	2.3	2.4	-0.41 ^b
<i>Ambystoma tigrinum</i>	2.1	2.8	2.2	2.8	3.0	4.0	2.0	3.4	3.0	4.0	2.9	2.6	3.4	2.1	2.9	Ns
<i>Notophthalmus viridescens</i>	0.0	0.0	1.3	1.5	1.0	1.8	2.0	3.3	1.0	5.0	1.8	2.5	2.8	1.3	1.8	0.48 ^c
<i>Siren intermedia</i>	0.0	0.0	3.0	1.0	4.0	2.0	0.0	1.7	1.0	1.5	2.3	2.3	1.0	1.0	1.5	ns
Anura	2.0	2.5	2.2	2.2	2.3	2.3	2.1	2.2	2.3	2.2	2.3	2.1	2.3	2.2	2.2	ns
Caudata	1.2	1.3	2.4	2.3	2.6	2.5	1.6	2.5	1.8	3.1	2.4	2.3	2.3	1.6	2.1	na
Total	1.8	2.2	2.3	2.2	2.4	2.4	2.0	2.3	2.1	2.5	2.3	2.2	2.3	2.0	2.2	ns

I used Kendal's Tau to detect non-parametric correlation of amphibian abundance, occupancy, and species richness, with time. Correlations were significant at $\alpha = 0.05$, and considered non-significant at $\alpha = 0.10$ level. I used stepwise multivariate logistic regression, ANOVA and MANOVA to model factors that best explained the variance in amphibian abundance, number of breeding sites, occupancy, and species richness, (Brodman et al. 2003; Price et al. 2005). Models used $\alpha = 0.05$ to assign significance. The first set of factors modeled was climate data that were obtained from the Rensselaer weather station (WeatherBug, Available from <http://weather.weatherbug.com/IN/Rensselaer-weather.html>, last accessed 29 April 2009). The climate variables were monthly departures from the mean for precipitation (mm) and mean temperature (C). Climate data associated with a given field season (March-July) extended from August in the year prior to the annual survey through the end of the survey period in July. A second set of factors was biotic associations of amphibian species within the community. The final set of factors was the degree of wetland clustering and isolation, and hydroperiod heterogeneity. I detected wetland clusters using GIS by creating 200-m core upland habitat around each wetland. Wetlands within 400 m of each other joined to form wetland clusters (Brodman et al. 2003). The rationale for this is that wetlands within 400 m have overlapping populations in the terrestrial environment (Semlitsch 1998; Brodman et al. 2003). Hydroperiod heterogeneity was high when a wetland cluster has wetlands in all three hydroperiod categories, seasonal, semi-permanent, and permanent. I

included ephemeral or saturated wetlands within the seasonal wetland category.

I used the GIS-based IBI Conservation Tool (Indiana Biodiversity Initiative, Bloomington, Indiana, USA) to map the largest amphibian metacommunities and landscape features. Landscape features include wetland clusters, and upland habitats with native plants of high conservation importance and wildlife umbrella species.

RESULTS

14 year trends.—We recorded 11,438 breeding populations in Jasper County from 1994 to 2007 (Tables 1–3). We found an average of 339 sites with amphibian breeding activity (Table 1), 817 populations (Table 1), 2.4 species per site (Table 1), and a breeding index score of 2.2 (Table 2). The years with the greatest abundance of amphibians were 2003, 1998, and 2004 and the lows were 1995, 1996, and 2006 (Table 3).

Some numbers of species increased during the study, whereas, others decreased. Time demonstrated a positive non-parametric correlation with the number of amphibian breeding sites, amphibian abundance, number of breeding sites, mean breeding index score, and with several parameters for individual species (*Rana pipiens*, *Siren intermedia*, *Bufo americanus*, *Acris crepitans*, and *Notophthalmus viridescens*; Tables 1–3). Time demonstrated a significant negative non-parametric correlation with species richness/site, mean breeding index score of seven anurans (*Pseudacris crucifer*, *P. triseriata*, *Hyla versicolor*, *H. chrysoscelis*, *B. fowleri*, *R. catesbeiana*, and *R. clamitans*), and the number of breeding sites and mean breeding index score of

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TABLE 3. Amphibian abundance in Jasper County, Indiana, USA from 1994-2007. Kendal's Tau indicated trends ($^{\circ}0.05 > P < 0.1$) and significant correlations ($^bP < 0.05$, $^cP < 0.01$, $^dP < 0.001$) with year.

	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	Mean	Tau
<i>Pseudacris crucifer</i>	458	341	338	767	1271	596	714	745	925	787	579	639	439	734	666.6	ns
<i>P. triseriata</i>	363	237	228	369	741	572	414	477	634	503	287	430	214	372	417.3	ns
<i>Hyla versicolor</i>	315	74	247	273	624	309	20	195	227	653	602	181	152	121	285.2	ns
<i>Hyla chrysoscelis</i>	49	21	46	58	40	18	104	33	17	79	54	52	4	49	44.6	ns
<i>Acris blanchardi</i>	0	0	0	0	0	5	6	14	25	46	93	11	12	29	17.2	0.7 ^d
<i>Bufo americanus</i>	192	89	56	157	541	324	61	222	521	556	150	214	362	515	276.4	0.36 ^b
<i>B. fowleri</i>	93	47	101	102	251	115	218	135	100	287	422	121	93	82	154.8	ns
<i>Rana pipiens</i>	42	33	13	23	31	37	23	59	50	62	76	21	98	62	45	0.42 ^b
<i>R. clamitans</i>	125	56	121	109	100	86	70	205	128	314	297	127	78	75	135.1	ns
<i>R. catesbeiana</i>	42	29	46	25	30	25	50	20	24	48	47	34	11	20	32.2	ns
<i>Ambystoma laterale</i>	19	21	24	16	15	13	5	3	2	9	16	12	10	18	13.1	-
<i>Ambystoma tigrinum</i>	19	22	11	17	12	8	6	17	9	12	38	21	27	27	17.6	0.33 ^b
<i>Notophthalmus viridescens</i>	0	0	4	3	1	9	2	10	1	5	9	5	14	5	4.9	0.49 ^c
<i>Siren intermedia</i>	0	0	3	1	8	2	0	3	1	3	7	9	2	3	3.0	0.40 ^b
Anura	1680	927	1196	1883	3539	2087	1680	2105	2651	3335	2607	1830	1463	2059	2074	ns
Caudata	38	43	42	37	36	32	13	33	13	29	70	47	53	53	38.5	ns
Total	1718	970	1238	1920	3575	2119	1693	2138	2664	3364	2677	1877	1516	2112	2112	ns

Ambystoma laterale (Tables 1 and 2). There was no correlation between time and any of the Tiger Salamander demographic metrics.

Community associations.—Regression modeling revealed a number of significant associations of species within the amphibian community (Table 4). The abundance of Spring Peepers (*Pseudacris crucifer*) and Eastern Grey Treefrogs (*Hyla versicolor*) explained 93.4% of the variation among years in abundance of other species, and a model that also included Blue-spotted Salamanders explained 96.4% of the variation in the abundance of other species. The abundance of Blanchard's Cricket Frogs (*Acris crepitans*), Eastern Gray Treefrogs, and Cope's Gray Treefrogs (*Hyla chrysoscelis*) explained 84.6% of the variation in the abundance of Fowler's Toads. The abundance of American Bullfrogs explained 75.2% of the variation in the abundance of Cricket Frogs. The abundance of Chorus Frogs explained 75.1% of the variation in the abundance of Spring Peepers. The abundance of Cricket Frogs and Eastern Gray Treefrogs explained 72.4% of the variation in the abundance of Green Frogs. The abundance of Northern Leopard Frogs and Blue-spotted Salamanders explained 60.9% of the variation in the abundance of Tiger Salamanders. The abundance of Spring Peepers and Northern Leopard Frogs explained 58.1% of the variation in the abundance of American Toads. The abundance of Fowler's Toads explained 54.2% of the variation in the abundance of Eastern Gray Treefrogs. The abundance of American Bullfrogs explained 51.7% of the variation in the abundance of Cope's Gray Treefrogs. The abundance of Eastern

Newts explained 45.4% of the variation in the abundance of Northern Leopard Frogs. The abundance of Spring Peepers and Tiger Salamanders explained 83.9% of the variation in the abundance of Chorus Frogs. The association was positive with Spring Peepers and negative with Tiger Salamanders.

Climate variables and amphibian abundance.—Regression modeling detected a significant effect of climate on amphibian abundance and breeding activity (Table 5). Precipitation from February through May, and temperature in September, February, and April through June, had the greatest influence. A regression model with precipitation, and temperature explained 90.4% of the variation among years in the number of sites with amphibian breeding activity. The relationship with number of sites was positive for temperature and negative for precipitation. A regression model with time, temperature and precipitation explained 80.0% of the variation in mean species richness per site. The relationship with species richness per site was positive for precipitation and negative for temperature and year.

A regression model with temperature and precipitation explained 59.5% of the variation in mean amphibian breeding index score. The relationship with breeding index was positive for precipitation and temperature. However the breeding index scores of frogs and salamanders differed. A regression model with temperature and precipitation explained 89.5% of the variation in mean breeding index score of frogs. The relationship was positive between frog temperature,

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TABLE 4. Significant community associations revealed by regression models. The abundance of amphibians (dependent variable) is explained by the abundance of predictor species. Values are regression coefficients (r^2), degrees of freedom (df), F statistics (F), and p values (P).

Dependent variable	Predictors	r^2	df	F	P
Amphibian community	Spring Peepers, Eastern Gray Treefrogs	0.966	2,13	77.8	< 0.001
Amphibian community	Spring Peepers, Eastern Gray Treefrogs, Blue-spotted Salamanders	0.982	3,13	88.4	< 0.001
<i>Pseudacris crucifer</i>	Chorus Frogs	0.905	1,13	36.3	< 0.001
<i>Pseudacris</i>	Spring Peepers, Tiger Salamanders	0.916	2,13	28.7	< 0.001
<i>Acris crepitans</i>	American Bullfrogs	0.867	1,13	16.7	< 0.001
<i>Hyla versicolor</i>	Fowler's Toads	0.736	1,13	14.2	0.003
<i>Hyla chrysoscelis</i>	American Bullfrogs	0.719	1,13	12.0	0.004
<i>Bufo fowleri</i>	Cricket Frogs, Eastern Gray Treefrogs, Cope's Gray Treefrogs	0.920	3,13	18.3	< 0.001
<i>Bufo americanus</i>	Spring Peepers, Northern Leopard Frogs	0.762	2,13	7.6	< 0.001
<i>Rana clamitans</i>	Cricket Frogs, Eastern Gray Treefrogs	0.851	2,13	14.4	0.001
<i>Rana pipiens</i>	Eastern Newts	0.674	2,13	10.0	0.008
<i>Ambystoma tigrinum</i>	Northern Leopard Frogs, Blue-spotted Salamanders	0.780	2,13	8.6	0.006

precipitation, and breeding index. A regression model with temperature, and precipitation explained 89.6% of the variation in salamander breeding index scores. The relationship with breeding index was positive between salamander breeding index and precipitation, but negative between breeding index and temperature.

A regression model with temperature and year explained 64.7% of the variation in mean breeding index scores of Chorus Frogs. The relationship with Chorus Frogs was positive for temperature and negative for time. Variation in climatic variables does not explain variation in Spring Peepers abundance or breeding activity. A regression model with temperature and time explained 65.4% of the variation in the number of sites with Cricket Frogs. In a second model temperature and precipitation and time explained 79.2% of the variation in the mean breeding index scores of Cricket Frogs, and in a third model precipitation explained 32.1% of the variation in the total abundance of Cricket Frogs. The relationship with Cricket Frogs was positive for time, and negative for temperature and precipitation.

A regression model with precipitation, temperature, and time explained 81.9% of the variation in mean breeding index scores of Eastern Gray Treefrogs. The relationship with Eastern Gray Treefrogs was positive for temperature, and negative for precipitation and time. Variation in climatic variables does not explain variation in Eastern Gray Treefrog abundance or breeding activity. Regression models with temperature explained 59.6% of the variation in the mean breeding index scores of Cope's Gray Treefrogs, 48.4% of the variation in the number of sites with Cope's Gray Treefrogs, and 49.4% of the variation in the total abundance of Cope's Gray Treefrogs. The relationship with Copes Gray Treefrogs was negative for temperature.

A regression model with precipitation explained 39.1% of the variation in mean breeding index scores of American Toads. The relationship with American Toads was positive for precipitation. Regression models with precipitation and temperature explained 91.2% of the

variation in the mean breeding index scores of Fowler's Toads, 66.1% of the variation in number of Fowler's Toad breeding sites, and 61.9% of the variation in the total abundance of Fowler's Toads. The relationship with Fowler's Toads was positive for temperature and negative for precipitation.

A regression model with time, temperature, and precipitation explained 89.3% of the variation in the number of sites with Northern Leopard Frogs. Regression models with precipitation explained 89.1% of the variation in total abundance, and 29.9% of the variation in the mean breeding index scores of Northern Leopard Frogs. The relationship with Northern Leopard Frogs was positive for time and precipitation, and negative for temperature.

A regression model with year and precipitation explained 72.0% of the variation in the mean breeding index scores of Green Frogs. Models with temperature explained 47.1% of the variation in the total abundance, and 44.1% of the variation in the number of sites with Green Frogs. The relationship with Green Frogs was positive for precipitation and negative for temperature and time. A regression model with precipitation, temperature, and time explained 99.5% of the variation in the mean breeding index scores of American Bullfrogs. A second model with temperature and precipitation explained 62.1% of the variation in the total abundance of American Bullfrogs, and a third model with temperature explained 33.5% of the variation in the number of sites with American Bullfrogs. The relationship with American Bullfrogs was negative for temperature, precipitation, and time.

A regression model with time and temperature explained 62.2% of the variation in the mean breeding index scores of Blue-spotted Salamanders. Models with precipitation explained 55.3% of the variation in the number of Blue-spotted Salamander breeding site, and 38.2% of the variation in the total abundance of Blue-spotted Salamanders. The relationship with Blue-spotted Salamanders was negative for temperature and

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TABLE 5. Influence of time and climate on amphibian abundance revealed by regression models. The number of amphibian breeding sites, species richness, and mean breeding index score, (dependent variable) is explained by the average monthly temperatures and precipitation, and time (predictors). Values are regression coefficients (r^2), degrees of freedom (df), F statistics (F), and p-values (P).

Dependent variable	Predictors	r^2	df	F	P
Amphibian breeding sites	Temperature, precipitation	0.951	2,13	15.1	0.001
Species richness	Time, temperature, precipitation	0.894	3,13	12.7	0.001
Amphibian breeding index	Temperature, precipitation	0.771	2,13	8.1	0.007
Frog breeding index	Temperature, precipitation	0.946	2,13	28.3	< 0.001
Salamander breeding index	Temperature, precipitation	0.947	2,13	19.3	< 0.001
Chorus Frog breeding index	Time, temperature	0.804	2,13	10.1	0.003
Cricket Frog breeding index	Time, temperature	0.809	2,13	10.4	0.003
Cricket Frog breeding index	Time, temperature, precipitation	0.890	3,13	10.8	0.001
Cricket Frog abundance	Precipitation	0.567	1,13	5.7	0.035
Eastern Gray Treefrog breeding index	Time, temperature, precipitation	0.905	3,13	15.1	< 0.001
Cope's Gray Treefrog breeding index	Temperature	0.772	1,13	9.1	0.001
Cope's Gray Treefrog breeding sites	Temperature	0.697	1,13	11.3	0.006
Cope's Gray Treefrog abundance	Temperature	0.703	1,13	11.7	0.005
American Toad breeding index	Precipitation	0.625	1,13	7.7	0.017
Fowler's Toad breeding index	Temperature, precipitation	0.955	2,13	23.4	< 0.001
Fowler's Toad breeding sites	Temperature, precipitation	0.813	2,13	10.7	0.003
Fowler's Toad abundance	Temperature, precipitation	0.787	2,13	8.9	0.005
Northern Leopard Frog breeding sites	Time, temperature, precipitation	0.945	3,13	18.8	< 0.001
Northern Leopard Frog abundance	Precipitation	0.944	1,13	18.3	< 0.001
Northern Leopard Frog breeding index	Precipitation	0.547	1,13	5.1	0.043
Green Frog breeding index	Time, precipitation	0.849	2,13	14.1	0.001
Green Frog abundance	Temperature	0.686	1,13	10.7	0.007
Green Frog breeding sites	Temperature	0.664	1,13	9.4	0.010
American Bullfrog breeding index	Time, temperature, precipitation	0.997	3,13	221.6	< 0.001
American Bullfrog abundance	Temperature, precipitation	0.788	2,13	9.0	0.005
American Bullfrog breeding sites	Temperature	0.579	1,13	6.1	0.030
Blue-spotted Salamander breeding index	Time, temperature	0.789	2,13	19.7	0.001
Blue-spotted Salamander breeding sites	Precipitation	0.744	1,13	7.4	0.012
Blue-spotted Salamander abundance	Precipitation	0.618	1,13	6.8	0.018
Tiger Salamander breeding sites	Temperature, precipitation	0.983	2,13	45.3	< 0.001
Tiger Salamander abundance	Precipitation	0.767	1,13	7.9	0.008
Tiger Salamander breeding index	Temperature	0.634	1,13	8.1	0.015
Eastern Newt abundance	Time, precipitation	0.871	2,13	10.5	0.002
Eastern Newt breeding sites	Time, temperature	0.846	2,13	8.4	0.004
Eastern Newt breeding index	Temperature	0.840	1,13	13.2	0.001
Lesser Siren sites	Precipitation	0.809	1,13	10.4	0.003

precipitation. A regression model with temperature, and precipitation explained 96.6% of the variation in the number of sites with Tiger Salamanders. A second model with precipitation explained 58.8% of the variation in the total abundance of Tiger Salamanders, and a third model with temperature explained 40.2% of the variation in the mean breeding index scores of Tiger Salamanders. The relationship with Tiger Salamanders was positive for precipitation and negative for temperature.

A regression model with time and precipitation explained 75.8% of the variation in the total abundance of Eastern Newts. A second model with time and temperature explained 71.5% of the variation in the number of sites with Eastern Newts, and a third model with temperature explained 70.6% of the variation in the

mean breeding index scores of Eastern Newts. The relationship with Eastern Newts was positive for temperature and time, and was negative for precipitation. A regression model with precipitation explained 65.5% of the variation in the number of sites with Lesser Sirens. The relationship between sirens and precipitation was positive.

From 1994 to 2007 the mean annual temperature was 3.55°C above average ($t_{11} = 3.63$; $P = 0.004$) and precipitation was 24.33 mm greater than average ($t_{11} = 0.52$; $P = 0.613$). However precipitation from September through December was significantly below average ($t_4 = -3.06$; $P = 0.038$). From 1994 to 2007 there were significant trends of increasing precipitation in August ($r^2 = 0.341$) and decreasing precipitation in June ($r^2 = 0.407$). Based on the climate trends of the last

TABLE 6. Post-hoc results for effects of wetland cluster size on amphibian metacommunities. Variables are the number of wetlands in a wetland cluster (WC), mean amphibian species richness (SR), mean community abundance (CA), and mean number of years with breeding activity (YA). The different superscripts indicate the subsets that are significantly different (Tukey HSD, post-hoc test, $\alpha = 0.05$). I show the F with df as ($F_{2,13}$) and p-values (P) from the MANOVA.

WC	SR	CA	YA
14 or more	7.2 ^a	139.4 ^a	10.1 ^a
2-13	4.9 ^b	38.6 ^b	5.9 ^b
1 (isolated)	3.3 ^c	14.6 ^c	3.1 ^c
$F_{2,13}$	3.6	27.5	3.1
P	0.028	<0.001	0.046

14 years, the regression models predict that Chorus Frogs, Eastern Gray Treefrogs, Fowler’s Toads and Eastern Newts benefit from increased temperature. However the models predict that Cricket Frogs, Cope’s Gray Treefrogs, Northern Leopard Frogs, Green Frogs, American Bullfrogs, Blue-spotted Salamanders, Tiger Salamanders, and overall species richness per breeding site will decrease from increased warming. The models also predict that reduced precipitation in June and during the fall will benefit Lesser Sirens and American Bullfrogs, but reduce Northern Leopard Frogs, Tiger Salamanders, Eastern Newts, and the mean species richness of breeding sites.

Metacommunities.—I identified 630 wetland clusters and isolated wetlands. Of these, 595 (94.4%) had at least one year with amphibian breeding activity and 512 (81.3%) had metacommunities with at least two coexisting species. Only 103 (16.3%) had amphibian breeding activity during 50% or more of the years. The number of wetlands within a wetland cluster significantly affected amphibian species richness, abundance, and the number of years with breeding activity. Wetland clusters of 14 or more wetlands had significantly greater, and isolated wetlands had significantly less species richness, total abundance of amphibians, and years with amphibian breeding activity

The abundance of all species, except Cricket Frogs, was significantly greater in wetland clusters of 14 or more, and within wetland clusters with all three hydroperiod classes than in isolated wetlands, smaller wetland clusters, or wetland clusters that lack one or two of the hydroperiod classes (Table 8). The abundance of Spring Peepers, Chorus Frogs, Eastern Gray Treefrogs, Cope’s Gray Treefrogs, American Toads, and Fowler’s Toads was also significantly less in isolated wetlands and in wetland clusters that had just one hydroperiod class than in wetland clusters with two hydroperiod classes.

I defined amphibian megametacommunities as the 23 wetland clusters with the greatest amphibian abundance. Collectively these metacommunities made up 42% of

TABLE 7. Post-hoc results for hydroperiod effects on amphibian metacommunities. Variables are the number of hydroperiod classes (HP), mean amphibian species richness (SR), mean community abundance (CA), and mean number of years with breeding activity (YA). Subsets that are significantly different (Tukey HSD, post-hoc test, $\alpha = 0.05$) are indicated with different superscripts. I show the F with df as ($F_{2,13}$) and p-values (P) from the MANOVA.

HP	SR	CA	YA
3	8.1 ^a	164.4 ^a	10.6 ^a
2	4.2 ^b	26.3 ^b	4.8 ^b
1	3.2 ^b	13.4 ^b	2.8 ^c
$F_{2,13}$	17.6	27.4	8.4
P	0.016	<0.001	<0.001

than wetland clusters with 2–13 wetlands (Table 6). The number of hydroperiod classes within a wetland cluster significantly affected amphibian species richness, abundance, and the number of years with breeding activity. Wetland clusters with permanent, semi-permanent and seasonal or temporary wetlands had significantly greater, and isolated wetlands had significantly less amphibian abundance, occupancy, and species richness than wetland clusters with only one or two of the hydroperiod classes (Table 7). There were also significant interactive affects of wetland clusters and hydroperiod on abundance ($F_{3,13} = 6.2, P < 0.001$), and number of years with amphibian breeding activity ($F_{3,13} = 3.3, P = 0.021$).

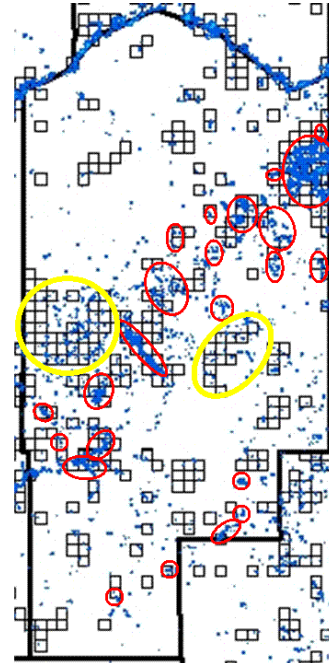


FIGURE 2. Map of Jasper County, Indiana, USA showing the location of 23 amphibian megametacommunities. Wetlands and isolated wetlands are indicated by blue squares, amphibian megametacommunities are indicated by red circles, and IBI priority habitats for important plants and umbrella animals are indicated by open squares. Yellow circles indicate areas with wetlands, and priority habitat, but no amphibian megametacommunities.

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TABLE 8. Wetland cluster size and hydroperiod effects on the abundance of amphibian species in Jasper County, Indiana, USA. Variables are mean abundance, the number of wetlands in a wetland cluster (WC), the number of hydroperiod classes (HP), and wetland cluster size and hydroperiod interactions (WC*HP). WC 1 = 1 isolated, 2 = 2–13 wetlands, 3 = 14 or more wetlands. HP1 = temporary/seasonal, HP2 = semipermanent, HP3 = permanent. Trends and significant differences detected by MANOVA are indicated by numerical superscripts (¹*P* < 0.1, ²*P* < 0.05, ³*P* < 0.01, ⁴*P* < 0.001) with year. Subsets that are significantly different (Tukey HSD, post-hoc test, $\alpha = 0.05$) are indicated with different alphabetical superscripts.

	Wetland Cluster			Hydroperiod			WC*HP		
	<i>F</i> _{2,629}	WC1	WC2	WC3	<i>F</i> _{2,629}	HP1	HP2	HP3	<i>F</i> _{3,629}
<i>Pseudacris crucifer</i>	21.7 ⁴	4.8 ^a	9.2 ^a	62.7 ^b	26.0 ⁴	5.2 ^a	13.4 ^b	53.8 ^c	4.5 ³
<i>P. triseriata</i>	24.8 ⁴	3.1 ^a	6.0 ^a	40.8 ^b	20.1 ⁴	3.4 ^a	8.9 ^b	33.4 ^c	6.7 ⁴
<i>Acrisblanchardi</i>	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.2	0.2
<i>Hyla versicolor</i>	23.9 ⁴	1.6 ^a	3.6 ^a	23.3 ^b	40.2 ⁴	1.8 ^a	5.1 ^b	21.6 ^c	12.9 ⁴
<i>H. chrysoscelis</i>	6.4 ³	0.2 ^a	0.8 ^a	4.5 ^b	5.4 ³	0.3 ^a	1.2 ^b	3.4 ^c	2.4 ¹
<i>Bufo americanus</i>	20.0 ⁴	1.8 ^a	3.0 ^a	18.8 ^b	17.6 ⁴	1.9 ^a	4.4 ^b	16.2 ^c	4.5 ³
<i>B. fowleri</i>	8.5 ⁴	1.0 ^a	1.6 ^a	9.7 ^b	20.8 ⁴	0.9 ^a	2.0 ^b	9.1 ^c	4.0 ³
<i>Rana pipiens</i>	17.4 ⁴	0.2 ^a	0.5 ^a	5.4 ^b	7.4 ³	0.2 ^a	0.8 ^a	3.6 ^b	4.6 ³
<i>R. clamitans</i>	8.2 ⁴	0.7 ^a	1.4 ^a	10.2 ^b	17.1 ⁴	0.8 ^a	2.0 ^a	9.1 ^b	4.4 ³
<i>R. catesbeiana</i>	14.3 ³	0.1 ^a	0.3 ^a	3.7 ^b	23.0 ⁴	0.1 ^a	0.5 ^a	3.3 ^b	17.3 ⁴
<i>Ambystoma laterale</i>	7.3 ³	0.1 ^a	0.1 ^a	10.4 ^b	3.3 ²	0.1 ^a	0.1 ^a	11.0 ^b	5.5 ³
<i>A. tigrinum</i>	16.6 ⁴	0.1 ^a	0.3 ^a	10.4 ^b	5.2 ³	0.1 ^a	0.2 ^a	10.6 ^b	8.2 ³
<i>Notophthalmus viridescens</i>	6.8 ³	0.0 ^a	0.0 ^a	3.9 ^b	3.0 ²	0.0 ^a	0.0 ^a	4.1 ^b	4.9 ³
<i>Siren intermedia</i>	7.6 ³	0.0 ^a	0.0 ^a	2.4 ^b	3.3 ²	0.0 ^a	0.0 ^a	2.6 ^b	5.5 ³

total amphibian abundance and had mean values of 9.3 species, 11.3 years with breeding activity, and amphibian abundance of 183. They had wetland clusters with a mean of 25.2 wetlands and 2.5 hydroperiod classes. These compare to mean values of 3.5 species, 3.5 years with breeding activity, amphibian abundance of 16.6, wetland clusters of 2.1 wetlands, and 1.2 hydroperiod classes for the other 607 sites. The megametacommunities are associated with several landscape variables (Fig. 2). Eighty percent of the 15 wetland clusters that have 14 or more wetlands and at least two of the three hydroperiod classes have amphibian megametacommunities. Three of eight (37.5%) of the wetland clusters with 2–13 wetlands and all three hydroperiod classes, and eight of 125 (6.4%) wetland clusters with 2–14 wetlands and two hydroperiod classes, are megametacommunities. None of megametacommunities were isolated wetlands, or clusters with just one hydroperiod class. Eighteen of the 23 (78%) megametacommunities include upland habitat identified by the IBI conservation tool as km² sections with greater than 50% cover by important native plants or core habitat for any of the six species designated for the region as umbrella wildlife species. The amphibian megametacommunities are associated with all but two of the large areas in Jasper County that have large numbers of wetlands and important native plant or umbrella animal habitats. The two exceptions are a 37 km² area near Parr, Indiana and a 12 km² area near Moody, Indiana, USA. While both areas have a large number of wetlands, they are mostly isolated or in small clusters that lack one or two of the hydroperiod classes.

DISCUSSION

14-year trends.—A combination of frog call surveys and breeding site surveys for salamanders, egg masses, larvae, and tadpoles, throughout Jasper County from 1994 to 2007 showed population fluctuations and relatively stable communities. Although I have published subsets of data from this long-term survey (Brodman and Kilmurry 1998; Brodman 2000a, 2000b; Brodman et al. 2002; Brodman 2003), this is the first long-term (> 10 years) county-wide survey of an entire amphibian community. Previous surveys in Jasper County focused only on the Jasper-Pulaski Fish and Wildlife Area and did not include call surveys or aquatic surveys of breeding sites (Grant 1936; Swanson 1939; Minton 1998). Several species (i.e., Chorus Frog, American Toad, Eastern Newt) were new county records found during this long-term survey (Brodman 2003). There are Jasper County records from the 1930's for Plains Leopard Frogs (*Rana blairi*), Smallmouth Salamanders (*Ambystoma texanum*) and Slimy Salamanders (*Plethodon glutinosus*; Grant 1936; Swanson 1939). Records of Crawfish Frogs (*R. areolata*), Wood Frogs (*R. sylvatica*), Pickerel Frogs (*R. palustris*), Redback Salamanders (*P. cinereus*), Four-toed Salamanders (*Hemidactylum scutatum*), Spotted Salamanders (*A. maculatum*), and Mudpuppies (*Necturus maculosus*) occur in adjacent counties (AmphibiaWeb, available from <http://www.amphibiaweb.org>, last accessed 27 April 2009). However, none of these species occurred in Jasper County during this 14-year survey. Based on anecdotes from fishermen, including some of my herpetology students, Mudpuppies are the only one of these species that is likely to be present in the county today.

The number of amphibian breeding sites (in total and for several species) increased, whereas mean species richness per site, and the mean population size (in total and for most species) decreased over a period of 14 years. Blanchard's Cricket Frog declined throughout the northern portion of its range, including northern Indiana, and was absent from Jasper County in the mid-1990's (Brodman and Kilmurry 1998; Minton 2001; Gray and Brown 2005; Gray et al. 2005). Moreover, the Northern Leopard Frog has continued to decline in northern and central Indiana and other parts of its range since the 1960's (Gibbs et al. 1971; Lannoo et al. 1994; Minton 2001; Rorabaugh 2005). Another species of special concern, the Blue-spotted Salamander, decreased in total abundance. Blue-spotted Salamanders have also declined in Illinois (Grant 1936; Smith 1961), Ohio, elsewhere in Indiana (Minton 2001; Brodman 2005), and throughout its range where native forests and wetlands have been replaced by agriculture and development (Petranka 1998). Fire management to open oak savanna canopy, and competition with Tiger Salamanders and unisexual populations could be factors in this decline (Jaskula and Brodman 2000; Brodman and Krouse 2007).

Community associations.—Biotic associations among amphibian species indicate that Spring Peepers and Eastern Gray Treefrogs were the best indicators of amphibian biodiversity. A smaller data set indicated that Green Frogs were also an indicator species (Brodman et al. 2002); whereas, the large data set suggests Blue-spotted Salamanders as a third bioindicator. Blue-spotted Salamanders were also identified as a bioindicator of the amphibian and reptile community in oak savanna habitat (Brodman et al. 2005). Spring Peepers and Eastern Gray Treefrogs are among the best indicators of forest habitat quality in Iowa and Wisconsin (Knutson et al. 2000). The strongest associations among amphibian species were among Fowler's Toads, Cricket Frogs, Eastern Gray Treefrogs, and Cope's Gray Treefrogs; between Cricket Frogs and American Bullfrogs; among Tiger Salamanders, Northern Leopard Frogs and Blue-spotted Salamander; and a negative relationship between Chorus Frogs and Tiger Salamanders. Most of these associations are between species with different spatial patterns of density within the county (Brodman 2000b), and a smaller data set indicated that co-variation with habitat characteristics were more important than most biotic interactions in explaining the associations (Brodman et al. 2003). However, it is likely that predation by salamanders is causing Chorus Frogs to avoid the breeding sites of Tiger Salamanders (Skelly 1996).

Climate variables and amphibian abundance.—Amphibian declines and population fluctuation can be related to climate (Brodman 2002; Daszak et al. 2005; Reaser and Blaustein 2005). In this study, climatic variation among years was more important than annual trends in explaining most amphibian population and community trends. After factoring for co-variation with climatic variables, time was not a factor in explaining overall amphibian population and community trends; however, time was an important factor for several species (Blanchard's Cricket Frogs, Northern Leopard Frogs, Eastern Newts) that increased, and for several species (Chorus Frogs, Eastern Gray Treefrogs, Green Frogs, American Bullfrogs) that decreased in at least one population demographic from 1994 to 2007.

Small changes in temperature and precipitation during parts of the year can have important biological consequences. Temperature and precipitation from February through June impact the quality and quantity of breeding sites and recruitment of juveniles (Lannoo 1998; Brodman 2002). Precipitation from August to November and temperature from October to February impact survival during hibernation and body condition during the breeding season (Bradford 1983; Irwin et al. 1999; Tonn et al. 2005).

Regional models indicate that temperature variation influences frogs more than other amphibians; whereas, precipitation is more influential with salamanders (Battaglin et al. 2005). However, in Jasper County, temperature and precipitation both influenced frogs and salamanders, although frogs did better in warmer years and salamanders did better in cooler years. Amphibians that are most at risk from global climate change are those at upper tolerance limits of temperature or dryness, depending on ephemeral or seasonal wetlands, and have barriers to dispersal (Reaser and Blaustein 2005). Many amphibians found in northwest Indiana are near their northern, southern (temperature), or western (dryness) limit of their range. The period during this study was warmer and wetter than normal, although it was also drier than normal from September to December. If these climatic trends continue, then this can become a factor for amphibian declines. Blue-spotted Salamanders, Tiger Salamanders, Cricket Frogs, Cope's Gray Treefrogs, Green Frogs, and Northern Leopard Frogs did worse in warmer years or in years with drier autumns. It is uncertain to the extent that agriculture and isolation of breeding sites act as barriers to dispersal.

Metacommunities.—This study provides data in support of the Lannoo Model (Lannoo 1998) that predicts that the number of wetlands and hydroperiod heterogeneity of wetlands influence amphibian abundance, occupancy, and diversity. Smaller data sets indicated that hydroperiod of wetlands within 1 km, number of wetlands within 1 km and 400 m, and non-

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agricultural upland habitat were among the most important factors influencing amphibian abundance and occupancy of breeding sites in Jasper County (Brodman and Killmurphy 1998; Brodman et al. 2003). At other study sites, vegetative cover within 1000 m (Mazerolle et al. 2005), number of wetlands within 500 m and 3000 m (Price et al. 2005), and hydrology of wetlands within a complex (Naugle et al. 2005) have also been shown to influence amphibian demographics. This study also supports the hypothesis that ephemeral and seasonal wetlands are ecologically important for the conservation of amphibian metapopulations because of their roles in habitat connectivity and successful recruitment of offspring during wet years (Lannoo 1998; Semlitsch and Bodie 1998; Naugle et al. 2005).

Landscape factors associated with large amphibian metacommunities include wetland clusters of 15 or more wetlands that have ephemeral/seasonal, semi-permanent and permanent hydroperiods, and upland habitat with important native vegetation. Expanding agriculture and development is expected to cause further habitat loss, fragmentation, wetland isolation, reduced hydroperiod heterogeneity, and degraded upland habitat. The primary land management recommendation is to restore or protect wetland complexes with 15 or more wetlands with connecting upland habitat. Wetlands need to vary in hydrology to create heterogeneity within the landscape. I have identified two locations in Jasper County that have wetlands and upland habitat, but lack connectivity. Large metacommunities of amphibians in these areas could be restored by creating clusters of nearby wetlands connected by upland corridors. Amphibian abundance and diversity increased exponentially to form an amphibian megametacommunity within the five years after the start of a large-scale habitat restoration at Kankakee Sands (30 km from Jasper County; Brodman et al. 2006). Habitat restoration there included creating wetland clusters with permanent, semi-permanent, and ephemeral/seasonal wetlands, and native upland vegetation connecting remnant populations.

Long-term studies of metacommunities and metapopulations at landscape spatial scales are valuable to ecological modeling and conservation designs (Cody 1996; Storfer 2003; Daszak et al. 2005; Whiteman and Wissinger 2005; Milne and Bennett 2007). Research and conservation efforts for pond-breeding amphibians need to focus on wetland clusters as land management units (Petranka et al. 2004). This 14-year study is intended to be an interim report of a long-term on-going study of the entire amphibian community in Jasper County, Indiana. The trends of amphibian populations and community dynamics detected over 14 years indicate that habitat characteristics at the landscape scale, and climate variables are important determinants of pond-breeding amphibian abundance and breeding.

Future aspects of this research program will focus on questions related to wetland clusters and metacommunity ecology.

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LITERATURE CITED

- Alexander, M.A., and J.K. Eischeid. 2001. Climate variability in regions of amphibian declines. *Conservation Biology* 15:930–942.
- Alford, R.A., P.M. Dixon, and J.H.K. Pechmann. 2001. Global amphibian population declines. *Nature* 412:499–500.
- Battaglin, W., L. Hay, G. McCabe, P. Nanjappa, and A. Gallant. 2005. Climatic patterns as predictors of amphibian species richness and indicators of potential stress. *Alytes* 22:146–147.
- Bradford, D.F. 1983. Winterkill, oxygen relations, and energy metabolism or a submerged dormant amphibian, *Rana muscosa*. *Ecology* 64:1171–1183.
- Brodman, R. 2000a. Field surveys of amphibian populations—investigative research on campus: an extension of classroom instruction. *Journal of College Science Teachers* 30:117–121.

- Brodman, R. 2000b. Differences among the spatial distribution of sympatric amphibians. *The Journal of the Iowa Academy of Science, Special Issue* 107:200–202.
- Brodman, R. 2002. A 12 year study monitoring two populations of Mole Salamanders in northeast Ohio. *Journal of the Ohio Academy of Science* 102:123–127.
- Brodman, R. 2003. Amphibians and reptiles from 23 counties of Indiana: Indiana Herp Atlas. *Proceedings of the Indiana Academy of Science* 112:43–54.
- Brodman, R. 2005. *Ambystoma laterale*, Blue-spotted Salamander. Pp 614–616 *In Amphibian Declines: The Conservation Status of United States Species*. Lannoo, M. (Ed.). University of California Press, Berkley, California, USA.
- Brodman, R. and M. Kilmurry 1998. The status of amphibians in rural northwest Indiana. Pp. 125–136 *In The Status and Conservation of Midwest Amphibians*. Lannoo, M.J. (Ed.). Iowa University Press, Iowa City, Iowa, USA.
- Brodman, R., and H. Krouse. 2007. How Blue-spotted Salamander and Smallmouth Salamander larvae coexist with their unisexual polyploid counterparts. *Herpetologica* 63:135–143.
- Brodman, R., S. Cortwright, and A. Reseatar. 2002. Historical changes of reptiles and amphibians of northwest Indiana fish and wildlife properties. *American Midland Naturalist* 147:135–144.
- Brodman, R., J. Ogger, A.P. Long, T. Bogard, R. Pulver, D. Falk, and K. Mancuso. 2003. Multivariate analyses of the influences of water chemistry and habitat parameters on the abundances of pond-breeding amphibians. *Journal of Freshwater Ecology* 18:425–436.
- Brodman, R., T. Anton, K. Glennmeier, P. Seth, D. Didion, and A. Luksus. 2005. Status of amphibians and reptiles in savanna habitats and savanna mosaic communities of the Chicago Wilderness Region. *Chicago Wilderness Journal* 3:38–44.
- Brodman, R., M. Parrish, H. Krause, M. Parrish, and S. Cortwright. 2006. Amphibian biodiversity recovery in a large-scale ecosystem restoration. *Herpetological Conservation and Biology* 1:101–108.
- Cody, M.L. 1996. Introduction to long-term community ecological studies. Pp. 1–15 *In Long-term Studies of Vertebrate Communities*. Cody, M.L., and J.A. Smallwood (Eds.). Academic Press, San Diego, California, USA.
- Cortwright, S.A. 1998. Ten to eleven-year population trends of two pond-breeding amphibian species, Red-spotted Newts and Green Frogs. Pp. 61–71 *In Status and Conservation of Midwestern Amphibians*. Lannoo, M.J. (Ed.). University of Iowa press, Iowa City, Iowa, USA.
- Crouch, W.B., and P.W.C. Paton. 2002. Assessing the use of call surveys to monitor breeding anurans in Rhode Island. *Journal of Herpetology* 36:185–192.
- Daszak, O., D.E. Scott, A.M. Kilpatrick, C. Faggioni, J.W. Gibbons, and D. Porter. 2005. Amphibian population declines at Savannah River site are linked to climate, not chytridiomycosis. *Ecology* 86:3232–3237.
- de Solla, S.R., K.J. Fernie, G.C. Barrett, and C.A. Bishop. 2006. Population trends and calling phenology of anuran populations surveyed in Ontario estimated using acoustic surveys. *Biodiversity and Conservation* 15:3481–3497.
- de Solla, S.R., L.J. Shirose, K.J. Fernie, G.C. Barrett, C.S. Brousseau, and C.A. Bishop. 2005. Effect of sampling effort and species detectability on volunteer based anuran monitoring programs. *Biological Conservation* 121:585–594.
- Diamond, J.M. 1996. Overview: Laboratory experiments, field experiments, and natural experiments. Pp. 3–22 *In Community Ecology*. Diamond, J.M., and T.J. Case (Eds.). Harper & Row, New York, New York, USA.
- Gibbons, J.W., V.J. Burke, J.E. Lovich, R.D. Semlitsch, T.D. Tuberville, J.R. Bodie, J.L. Greene, P.H. Niewiarowski, H.H. Whiteman, D.E. Scott, J.H.K. Pechmann, C.R. Harrison, S.H. Bennet, J.D. Krenz, M.S. Mills, K.A. Buhlmann, J.R. Lee, R.A. Seigel, A.D. Tucker, T.M. Mills, T. Lamb, M.E. Dorcas, J.D. Congdon, M.H. Smith, D.H. Nelson, M.B. Dietsch, H.G. Hanlin, J.A. Ott, and D.J. Karapatakis. 1997. Perceptions of species abundance, distribution, and diversity: Lessons from four decades of sampling on a government-managed reserve. *Environmental Management* 21:259–268.
- Gibbs, E.L., G.W. Nance, and M.B. Emmons. 1971. The live frog is almost dead. *BioScience* 21:1027–1034.
- Grant, C. 1936. Herpetological notes from northern Indiana. *Proceedings of the Indiana Academy of Science* 4:244–246.
- Gray, R.H., and L.E. Brown. 2005. Declines of Northern Cricket Frogs (*Acris crepitans*). Pp. 47–54 *In Amphibian Declines: The Conservation Status of United States Species*. Lannoo, M. (Ed.). University of California Press, Berkley, California, USA.
- Gray, R.H., L.E. Brown, and L. Blackburn. 2005. *Acris crepitans*, Northern Cricket Frog. Pp. 441–443 *In Amphibian Declines: The Conservation Status of United States Species*. Lannoo, M. (Ed.). University of California Press, Berkley, California, USA.
- Hairston, N.G. 1996. Predation and competition in salamander communities in long term studies of vertebrate communities. Pp. 161–189 *In Long-Term Studies of Vertebrate Communities*. Cody, M.L., and J.A. Smallwood (Eds.). Academic Press, San Diego, California, USA.

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- Hastings, A., and C.L. Wolin. 1989. Within-patch dynamics in a metapopulation. *Ecology* 70:1261–1266.
- Houlahan J.E., C.S. Findlay, B.R. Schmidt, A.H. Meyer, and S.L. Kuzmin. 2000. Quantitative evidence for global amphibian population declines. *Nature* 404:752–755.
- Irwin, J.T., J.P. Costanzo, and R.E. Lee. 1999. Terrestrial overwintering in the Northern Cricket Frog, *Acris crepitans*. *Canadian Journal of Zoology* 77:1240–1246.
- Jaskula, J.M., and R. Brodman. 2000. Density-dependent effects on microhabitat selection and activity of two species of larval *Ambystoma* salamanders. *The Journal of the Iowa Academy of Science, Special Issue* 107:146–150.
- Karns, D.R. 1986. *Field Herpetology: Methods for the Study of Amphibians and Reptiles in Minnesota*. James Ford Bell Museum of Natural History, Occasional Paper Number 18. 88 p.
- Kiesecker, J.M., A.R. Blaustein, and L.K. Beldon. 2001. Complex causes of amphibian population declines. *Nature* 410:681–684.
- Knutson, M.G., J.R. Sauer, D.A. Olsen, M.J. Mossman, L.M. Hemesath, and M.J. Lannoo. 2000. Landscape associations of frog and toad species in Iowa and Wisconsin, U.S.A. *Journal of the Iowa Academy of Science, Special Issue* 107:134–145.
- Lannoo, M.J., K. Lang, T. Waltz, and G.S. Phillips. 1994. An altered amphibian assemblage: Dickinson County Iowa, 70 years after Frank Blanchard's survey. *American Midland Naturalist* 131:311–319.
- Lannoo, M.J. 1998. Amphibian conservation and wetland management in the Upper Midwest: a catch-22 for the Cricket Frog? Pp. 330–339 *In* *The Status and Conservation of Midwest Amphibians*. Lannoo, M.J. (Ed.). Iowa University Press, Iowa City, Iowa, USA.
- Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943–1967.
- Lindsey, A.A., D.V. Schmelz, and S.A. Nichols. 1969. *Natural Areas in Indiana and Their Preservation*. Indiana Academy of Science, Indianapolis, Indiana, USA.
- MacArthur, R.H., and E.O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- MacKenzie, D.I., J.D. Nichols, G.B. Lachman, S. Droege, J.A. Royle, and C.A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255.
- Mazerolle, M.J., A. Desrochers, and L. Rochefort. 2005. Landscape characteristics influence pond occupancy by frogs after accounting for detectability. *Ecological Applications* 15:824–834.
- Milne, R.J., and L.P. Bennett. 2007. Biodiversity and ecological value of conservation lands in agricultural landscapes of southern Ontario, Canada. *Landscape Ecology* 22:657–670.
- Minton, S.A. 1998. Observations on Indiana amphibian populations: A forty-five-year overview. Pp. 217–220 *In* *Status and Conservation of Midwestern Amphibians*. Lannoo, M.J. (Ed.). University of Iowa Press, Iowa City, Iowa, USA.
- Minton, S.A. 2001. *Amphibians and Reptiles of Indiana*. Indiana Academy of Science, Indianapolis, Indiana, USA.
- Mossman, M.J., L.M. Hartman, R. Hay, J.R. Sauer, and B.J. Dhuey. 1998. Monitoring long-term trends in Wisconsin frog and toad populations. Pp. 169–198 *In* *Status and Conservation of Midwestern Amphibians*. Lannoo, M.J. (Ed.). University of Iowa Press, Iowa City, Iowa, USA.
- Naugle, D.E., K.F. Higgins, R.R. Johnson, T.D. Fischer, and F.R. Quamen. 2005. Landscape Ecology. Pp. 185–192 *In* *Amphibian Declines: The Conservation Status of United States Species*. Lannoo, M. (Ed.). University of California Press, Berkeley, California, USA.
- Pechmann, J.H.K., D.E. Scott, R.D. Semlitsch, J.P. Caldwell, L.J. Vitt and J.W. Gibbons. 1991. Declining amphibian populations: The problem of separating human impacts from natural fluctuations. *Science* 253:892–895.
- Petranka, J.W. 1998. *Salamanders of the United States and Canada*. Smithsonian Institution Press, Washington, D.C., USA.
- Petranka, J.W., C.K. Smith, and A.F. Scott. 2004. Identifying the minimal demographic unit for monitoring pond-breeding amphibians. *Ecological Applications* 14:1065–1078.
- Pierce, B.A., and K.J. Gutzwiller. 2004. Auditory sampling of frogs; Detection efficiency in relation to survey duration. *Journal of Herpetology* 38:495–500.
- Pieterston, E.C., L.M. Addison, J.N. Agobian, B. Brooks-Solveson, J. Cassani, and E.M. Everham, III. 2006. Five years of the southwest Florida Frog Call Monitoring Network: Changes in frog communities as an indicator of landscape change. *Florida Scientist* 69(suppl.):117–126.
- Pounds, J.A., M.R. Bustamante, L.A. Coloma, J.A. Consuegra, M.P.L. Fogden, P.N. Foster, E. La Marca, K.L. Masters, A. Merino-Viteri, R. Puschendorf, S.R. Ron, G.A. Sanchez-Azofeifa, C.J. Still, and B.E. Young. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* 439:161–167.
- Price, S.J., D.R. Marks, R.W. Howe, J.M. Hanowski, and G.J. Niemi. 2005. The importance of spatial scale for conservation and assessment of anuran populations in coastal wetlands of the western Great Lakes, USA. *Landscape Ecology* 20:441–454.

Herpetological Conservation and Biology

- Reaser, J.K., and A. Blaustein. 2005. Repercussions of global change. Pp. 60–63 *In* Amphibian Declines: The Conservation Status of United States Species. Lannoo, M. (Ed.). University of California Press, Berkeley, California, USA.
- Rorabaugh, J.C. 2005. *Rana pipiens*, Northern Leopard Frog. Pp 570–577 *In* Amphibian Declines: The Conservation Status of United States Species. Lannoo, M. (Ed.). University of California Press, Berkeley, California, USA.
- Seigel, R.A., R.B. Smith, J. Demuth, M. Ehrhart-Lwellelyn, and F.F. Snelson. 2002. Amphibians and reptiles of the John F. Kennedy Space Center, Florida: A long-term assessment of a large protected habitat. *Florida Scientist* 65:1–12.
- Semlitsch, R.D. 1998. Biological delineation of terrestrial buffer zones for pond-breeding salamanders. *Conservation Biology* 12:1113–1119.
- Semlitsch, R.D., and J.R. Bodie. 1998. Are small, isolated wetlands expendable? *Conservation Biology* 12:1129–1133.
- Semlitsch, R.D., D.E. Scott, J.H.K. Pechmann, and J.W. Gibbons. 1996. Structure and dynamics of an amphibian community: Evidence from a 16-year study of a natural pond. Pp. 217–250 *In* Long-term Studies of Vertebrate Communities. Cody, M.L., and J.A. Smallwood (Eds.). Academic Press, San Diego, California, USA.
- Sexton, O.J., C.A. Phillips, T.J. Bergman, E.B. Wattenberg, and R.E. Preston. 1998. Abandon not hope: Status of repatriated populations of Spotted Salamanders and Wood Frogs at the Tyson Research Center, St. Louis County, Missouri. Pp. 340–344 *In* Status and Conservation of Midwestern Amphibians. Lannoo, M.J. (Ed.). University of Iowa press, Iowa City, Iowa, USA.
- Skelly, D.K. 1996. Pond drying, predators, and the distribution of *Pseudacris* tadpoles. *Copeia* 1996:599–605.
- Skelly, D.K., E.E. Werner, and S.A. Cortwright. 1999. Long-term distributional dynamics of a Michigan amphibian assemblage. *Ecology* 80:2326–2337.
- Smith, P.W. 1961. The amphibians and reptiles of Illinois. *Illinois Natural History Survey Bulletin* 28:1–298.
- Spellerberg, I.F. 1991. *Monitoring Ecological Change*. Cambridge University Press, Cambridge, UK.
- Stevens, C.E., and C.A. Paszkowski. 2004. Using chorus-size ranks from call surveys to estimate reproductive activity of the Wood Frog (*Rana sylvatica*). *Journal of Herpetology* 38:404–410.
- Storfer, A. 2003. Amphibian declines: future directions. *Diversity and Distributions* 9:151–163.
- Stuart, S.N., J.S. Chanson, N.A. Cox, B.E. Young, A.S.L. Rodrigues, D.L. Fischman, and R.W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. *Science* 306:1783–1786.
- Swanson, P.L. 1939. Herpetological notes in Indiana. *American Midland Naturalist* 22:684–695.
- Tonn, W.M., B.R. Eaton, C.A. Paszkowski, A.J. Danylchuk, and S.M. Boss. 2005. Indirect effects of fish winterkills on amphibian populations in boreal lakes. *Canadian Journal of Zoology* 83:1532–1539.
- Whiteman, H.H., and S.A. Wissinger. 2005. Amphibian population cycles and long-term data sets. Pp. 177–184 *In* Amphibian Declines: The Conservation Status of United States Species. Lannoo, M. (Ed.). University of California Press, Berkeley, California, USA.
- Wilson, D.S. 1992. Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. *Ecology* 73:1984–2000.
- Woinarski, J.C.Z., J.C. McCosker, G. Gordon, B. Lawrie, C. James, J. Augusteyn, L. Slater, and T. Danvers. 2006. Monitoring change in the vertebrate fauna of central Queensland, Australia, over a period of broad-scale vegetation clearance, 1973–2002. *Wildlife Research* 33:263–274.



BOB BRODMAN is a Professor of Biology and Environmental Science, and Chair of the Biology Department at Saint Joseph's College in Indiana, USA 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 at Victoria University of Wellington, New Zealand, with Spike the Tuatara (*Sphenodon punctatus*). He received his Ph.D. in Ecology from Kent State University working under Dr. Lowell P. Orr. Prior to publishing this 14-year study, Bob had previously published the results of a 12-year study of salamander populations in Ohio. Bob believes that he cannot possibly be old enough to have done two long-term studies, but the math suggests otherwise. He is currently the senior Midwest co-chair of Partners for the Conservation of Amphibians and Reptiles, and has organized the first ever Herpetological Conservation & Biology Symposium for the 6th World Congress of Herpetology in Brazil (August 2008).