


Amphibians in forest pools: Does habitat clustering affect community diversity and dynamics?

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Abstract. Hydrologically isolated forest pools, both vernal and permanent, are receiving increased attention in conservation because they often provide fishless habitats for forest-dwelling amphibians, reducing risk of predation to eggs and larvae. However, clarifying conservation value of such pools requires determination of whether the species they contribute to local biodiversity are unique or also present in other nearby wetlands such as freshwater marshes. We compared composition of amphibian communities in clustered pools to that of both spatially isolated pools and freshwater marshes in Illinois (USA) from 2008 to 2010 to determine (1) effects of clustering on community structure, species richness, and occupancy dynamics; (2) unique contributions of forest pools (six clustered and three isolated pools) to amphibian diversity compared to marshes ($n = 6$); and (3) species-specific probabilities of occupancy by wetland type. Amphibian communities differed among wetland categories, with community similarity in the same year reduced 38% by differences between marshes, clustered pools, and isolated pools. Species richness was similar in clustered pools and marshes, but lower in isolated pools. Clustered pools contributed more species ($n = 10$) than marshes ($n = 7$) or isolated pools ($n = 4$). Anuran species had higher probability of greater relative abundance and salamanders had greater probability of encounter at clustered pools than at isolated pools, and probabilities of species-specific site occupancy were lowest at isolated pools. Wildlife managers in Midwest USA can better understand species-specific occupancy dynamics of amphibians in different wetland categories through this analysis and can optimize local amphibian species richness through conservation of clusters of forest pools.

Key words: community similarity; forest amphibians; habitat clustering; habitat isolation; Illinois; species richness.

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INTRODUCTION

Amphibians are declining worldwide, mainly from loss or degradation of habitat (Preisser et al. 2000, Stuart et al. 2004, Petranka and Holbrook 2006, Gallant et al. 2007). Losses have been severe in the U.S. Midwest, where 90% of pre-settlement

wetlands have been converted to agricultural and other uses (Dahl 1990). In this region and globally, emphasis has shifted from species conservation to habitat conservation (Petranka and Holbrook 2006) because extinction probability for individual species increases with loss of terrestrial habitat surrounding wetlands (Harper et al.

2008). Among habitats important to amphibians in temperate deciduous forests are hydrologically isolated permanent pools and vernal pools: small, shallow bodies of water occupying topographic depressions adjacent to or within a forest. Such pools normally have no regular inflow or outflow of water. This condition often renders the pools fishless, creating habitats of reduced predation risk for amphibian eggs and larvae, an obligate condition for some species (Porej and Hetherington 2005, Petranka and Holbrook 2006).

The persistence of a given assemblage of amphibian species depends not only on quantity of habitat, but also on sufficient connectivity among separate breeding populations (Guerry and Hunter 2002, Harper et al. 2008), making the landscape density of wetlands a critical variable in maintaining amphibian communities and individual populations that comprise them (Ficetola et al. 2009). Current opinion regarding habitat arrangement would predict that communities in clustered habitats should support greater species richness and subpopulations of individual species should be more persistent than those in isolated habitats because clustered habitats should have greater connectivity (exchange of individuals among different habitat patches), a prediction verified in theoretical studies using habitat simulation models that can separate effects of habitat loss from those of habitat fragmentation and isolation (Fahrig 1997, 2002, 2003, Flather et al. 2002). Although comprehensive studies of amphibian populations have found no relationships between wetland size and species richness (Snodgrass et al. 2000a), models specific to U.S. Midwest amphibians have shown some species to be sensitive to dispersal distance (Rustigian et al. 2003) and “functional connectivity” of wetlands, the level of resistance to amphibian dispersal in surrounding habitats (Compton et al. 2007). Such findings suggest that amphibian populations are sensitive to wetland isolation, a prediction supported in field studies showing that increased isolation of wetlands reduced colonization events (Skelly et al. 1999) and can cause decreased species richness in amphibian communities (Mann et al. 1991, Vos and Stumpel 1995, Lehtinen et al. 1999).

Compared to isolated habitats, extinction of a subpopulation at one site in a cluster of similar habitats would theoretically have a greater probability of reversal through demographic rescue by

re-colonization from subpopulations in adjacent sites in the cluster. This prediction, however, has rarely been tested empirically in natural environments (e.g., Werner et al. 2009). If clustered habitats increase population persistence and community diversity compared to isolated habitats, then conservation of such populations should consider the spatial proximity and connectivity of habitats as a relevant variable in management (Compton et al. 2007). In landscapes where natural areas are fragmented by anthropogenic disturbances, the degree of clustering of specific habitats within remaining natural areas could mitigate adverse effects of fragmentation, including decline and local extirpation of site-specific populations. Clustering might prove especially important for species that possess limited dispersal ability and specialized habitat needs, which is the case for many species of amphibians.

We investigated the effect of clustering of hydrologically isolated, permanent forest pools on amphibian species richness, community diversity, and species occupancy dynamics in forest preserves in DuPage County, Illinois (USA), to determine whether spatial proximity of pools would affect composition of communities or the probability of occupancy, colonization, or extinction by particular species. We also examined freshwater marshes in the same landscapes to determine whether species present in forest pools were consistently present only in such pools or present in both pools and marshes in this landscape. We considered such comparison necessary for assessment of the comparative value of such pools to other wetland habitats in this setting. The fundamental questions we addressed were (1) do clustered pools display greater amphibian species richness, species occupancy, and species abundance than isolated pools, (2) are amphibian species in forest pools complementary to or redundant of those in marshes in the same landscape, and (3) do species-specific probabilities of occupancy, colonization, and extinction differ by species and wetland type? By answering these questions, we sought to evaluate theoretical predictions about effects of habitat clustering on species richness and community diversity as applied to particular communities in a natural environment. We also hoped to provide managers with information that could be used to assess the importance of spatial proximity of pools on amphibian community composition,

enabling more informed decisions in prioritizing individual pools or pool clusters as targets of conservation effort.

STUDY AREA

History, climate, and vegetation

The DuPage Forest Preserve District (DFP) in DuPage County of northeastern Illinois, USA (41°49' N 88°05' W), was established in 1915 by citizens to protect natural areas in their communities. As of 2010, there were over 60 preserves protecting approximately 10,200 ha containing protected wetlands, forests, and prairies, approximately 12% of the land area within DuPage County.

DuPage County, like surrounding northeastern Illinois, has a seasonal climate. In the 20 years prior to the beginning of the study in 2008 (1988–2007), average annual maximum temperature at Illinois State Climatologist Weather Station 119221 (Wheaton, Illinois, USA) was 30.6°C, usually occurring in July. Average annual minimum temperature was –9.2°C, usually occurring in January. Average annual precipitation was 151.6 cm (90.4 cm rainfall, 61.2 cm snowfall), with driest months being September and October and wettest being January and February (Illinois State Water Survey 2011). Rainfall increases from March through June, with temperatures moving above freezing by March, creating favorable conditions for filling of forest pools in synchrony with the breeding periods of amphibians.

Forests surrounding the pools were dominated by American elm (*Ulmus americana*), maples (*Acer* spp.), black oak (*Quercus velutina*), basswood (*Tilia americana*), hickories (*Carya* spp.), viburnums (*Viburnum* spp.), and dogwoods (*Cornus* spp.). Woody vegetation in marshes was dominated by black ash (*Fraxinus nigra*), buttonbush (*Cephalanthus occidentalis*), and white oak (*Quercus alba*). Emergent vegetation in marshes was dominated by cattails (*Typha* spp.), tussock sedge (*Carex stricta*), and various species of rushes (*Juncus* spp.).

Regional and local amphibian biodiversity

By global standards, amphibian biodiversity within the U.S. Great Lakes region, including northeastern Illinois, is low, with amphibians reaching current levels of regional biodiversity only within the last 12,000 (Harding 1997). Preserves in the DFP are typical of the herpetofaunal

region described as the Northeastern Illinois Mesic Forest (Vestal 1931, Smith 1961) and are the last remnants of such forests in DuPage County. Amphibians resident in the DFP were represented by orders Anura (frogs and toads) and Caudata (salamanders) and contained species characteristic of current regional assemblages, including 16 regionally abundant species, some approaching their northern distributional limits (Smith 1961, Harding 1997). Of 19 species of salamanders and 21 species of anurans known to have historically occurred in Illinois (Smith 1961), the DFP contained five salamander species and 11 anuran species, species richness similar to comparably sized protected areas in other parts of the U.S. Great Lakes region (e.g., Skelly et al. 1999). The most historically common salamander species within the DFP have been eastern newt (*Notophthalmus viridescens*) and eastern tiger salamander (*Ambystoma tigrinum*), with spotted salamander (*Ambystoma maculatum*) and blue-spotted salamander (*Ambystoma laterale*) found less commonly in individual preserves. A fifth species, the mud puppy (*Necturus maculosus*), was native to larger river systems in DFP. Common anuran species in DFP included American bullfrog (*Lithobates catesbeianus*), American toad (*Anaxyrus americanus*), Cope's treefrog (*Hyla chrysoscelis*), gray treefrog (*Hyla versicolor*), green frog (*Lithobates clamitans*), northern leopard frog (*Lithobates pipiens*), spring peeper (*Pseudacris crucifer*), and western chorus frog (*Pseudacris triseriata*). The pickerel frog (*Lithobates palustris*), once common in DFP, has become less abundant, possibly in response to loss of preferred habitats of bogs and fens (DFP 2016). Although historically abundant, Blanchard's cricket frog (*Acris crepitans blanchardii*) and wood frog (*Lithobates sylvatica*) disappeared from DFP in 1974 and 1996, respectively (E. Neidy, DFP, personal communication). Common and scientific names follow Crother (2008).

METHODS

Site selection

Prior to our study, the DFP had classified 219 sites as wetlands within its preserves (D. Thompson, unpublished data). In an initial examination of this database in 2006, we eliminated 121 sites, including wetlands associated with prairies and meadows (40 sites), monoculture (*Typha* spp.)

marshes (27 sites), tree- and shrub-dominated marshes (five sites), lakes (18 sites), immature forests or monoculture forest plantations or nurseries (20 sites), actively managed reforestation of non-forest habitat (five sites), proximity to residential or office complexes or heavily used visitation areas (three sites), rivers and streams (two sites), and fens (one site). From the remaining 98 wetlands, we identified nine candidate marshes, defining these as permanent palustrine wetlands with inflows and outflows dominated by emergent vegetation without significant forest canopy above open-water areas (Cowardin et al. 1979).

In forested areas, the remaining 89 sites were considered for selection as clustered or isolated pools. Using satellite images, we located and inspected candidate wetlands on the ground to ensure that a pool or pool cluster was present and possessed characteristics described by Colburn (2004). Necessary characteristics were that a site was within a wooded area, beneath an overstory forest canopy, formed in a shallow depression primarily from runoff or groundwater rather than surface stream inputs, and had accumulated leaves and detrital material from surrounding forest.

We considered a site for inclusion in the category of “clustered pools” if two or more pools were within 100 m of their nearest neighbor, a distance that has included most designated “clusters” in past studies where clusters were identified as the minimal demographic unit of the population (Petranka et al. 2004). At such distances, we considered pools in a cluster to be “connected” because they were within dispersal distances of all local amphibian species. A pool was considered an “isolate” if there was no other pool ≤ 500 m from it. Although pools separated by greater distances might be within dispersal range of some species of forest-dwelling amphibians, the “life zone” for many pool-breeding amphibian species is < 200 m (Semlitsch 2000, Baldwin et al. 2006a, b). Most adult amphibians show strong fidelity to natal areas and maintain such fidelity through multiple breeding seasons (Semlitsch 2000, Smith and Green 2005, Gamble et al. 2007), limiting their movements to relatively short distances around breeding sites (Baldwin et al. 2006b), with most dispersing individuals moving ≤ 500 m from natal sites (Semlitsch 1998, Calhoun et al. 2005, Smith and Green

2005, Gamble et al. 2007). Such movement patterns are consistent with similarly low average dispersal and maximum movement distances reported in studies for salamanders and anurans as well as in comprehensive reviews of such studies (Gibbs 2000, Smith and Green 2005, Baldwin et al. 2006a).

Similarly, studies of landscape features associated with anuran populations have shown that even the most important habitat and landscape correlates of species presence and community composition lose significance at distances of > 500 m from breeding areas, indicating that it is within this distance that anurans interact with landscape features surrounding their breeding pools (Baldwin et al. 2006b, Eigenbrod et al. 2008). Other investigators have used greater distances to define isolated pools in contiguous habitat, but considered pools as isolated at smaller distances when intervening areas posed barriers to dispersal (Petranka et al. 2004), as was the case in our study where individual preserves were separated by high-traffic paved roads, human residential developments, and commercial and industrial areas.

After removal of sites not meeting our criteria, the remaining number of candidate sites was small (≤ 10 , all categories). Because wetlands generally, and forest pools in particular, can be variable in characteristics that affect amphibian community composition, we did not select remaining sites randomly, but consulted scientists of the DFP to identify those they considered most representative of each category and, within a category, most similar to one another in size, hydrology, and topography. We further narrowed our candidate group of potential pools to include only those with uniformly similar characteristics of being depressions, permanently flooded (over a one-year period of observation) areas with no observable anthropocentric modifications to their hydrology, and $> 50\%$ of open water covered by forest canopy. We considered only pools that were fishless, as determined by fish surveys of the DFP (D. Thompson, *unpublished data*) and on-site visual inspection. Selected isolated pools ranged from 0.1 to 0.5 ha, and selected clusters had combined open-water areas of 0.3–1.5 ha with two or three pools per cluster. Selected marshes ranged from 4 to 31 ha in size and had ≥ 4 ha of open water. Fish, such as bluegill and sunfish

(*Lepomis* spp.), bullhead (*Ameiurus* spp.), American pickerel (*Esox americanus*), and largemouth bass (*Micropterus salmoides*), were present in marshes and could act as predators on amphibians in all life stages. We did not control for effects of fish predation compared to the absence of such predation in forest pools, but note it as a possible mechanism for differences in species richness and community composition between wetland categories, in addition to differences attributable to habitat and hydrology (Kats et al. 1988, Hecnar and McCloskey 1997).

Amphibian surveys

Sampling began with ice breakup on pools and marshes in early March and continued through early July at all sites from 2008 to 2010, covering breeding periods of all local amphibian species. Salamanders were detected using minnow traps set in pools and marshes. Two or three traps were placed in each pool, depending on pool size, and three in each marsh. To ensure independence between traps, traps in pools were normally placed as far from one another as possible, with actual distances varying according to size of pool and extent of shallow water areas, but always ≥ 25 m apart (shoreline distance). Traps in marshes were placed at intervals of >100 m from one another, except in areas where shallow water was limited to one portion of the marsh. Traps were placed and checked on two to three consecutive nights each week at selected pools and marshes during sampling periods, but were removed from the marsh or pool on all other days in each week to prevent mortality of amphibians or other animals that might enter the trap and to reduce risk of trap theft. Species present in traps were identified and released with minimal or no handling according to protocols previously approved by the Wheaton College Animal Care and Use Committee in 2008 and reviewed annually through 2010 (Protocol S10-007).

Presence and relative abundance of anuran species were determined by calling surveys conducted once or twice weekly at each site, depending on weather conditions and differences in breeding seasons of specific amphibian species using particular sites. Surveys followed protocols used by the North American Amphibian Monitoring Program (Weir 2001) and so began ≥ 30 minutes after sunset and were terminated

before 01:00 hours under acceptable weather conditions (Weir 2001). Calling surveys will not detect the presence of all individual amphibians, but do detect male anurans in breeding readiness and thus reliably indicate the presence of breeding individuals. We used results of trapping and calling surveys to determine species richness of each site.

Visual encounter surveys (VES) are often used to estimate presence and relative abundance in amphibian studies (Crump and Scott 1994). We chose not to employ VES because it is only reliable for forest understory anurans active in the open and during daylight hours, traits that did not fit most of our species, and because estimates of presence and abundance from VES are not reliable without support of mark and recapture efforts or installation of drift net pitfall traps in the sampled area (Crump and Scott 1994, Nelson and Graves 2004, de Solla et al. 2005).

Sampling units

To compare wetland categories appropriately in our experimental design, we considered each selected site to be a single sampling unit consisting of one isolated pool, one cluster of pools, or one marsh. Applying these categories to our subset of wetlands meeting previously defined criteria and with comparable hydrologic and habitat features, we selected five clusters, five isolated pools and five marshes, the maximum number possible from available sites that provided a balanced design without introducing significant site-specific differences within or among wetland categories. Given the importance of independence among sites, we selected our sampling units in eight widely separated, non-contiguous preserves (Fig. 1). In addition to these sites, we also included two pool clusters and one marsh with similar characteristics to our originally selected pool clusters and marshes, and that were sampled by DFP following protocols of sampling intensity similar to ours, therefore meeting our criteria for sampling effort necessary to produce reliable estimates of species presence and abundance. After sampling began in 2008, we removed one cluster that experienced high levels of anthropogenic disturbance associated with its proximity to a residential neighborhood and new housing development. We removed two isolated pools because one dried

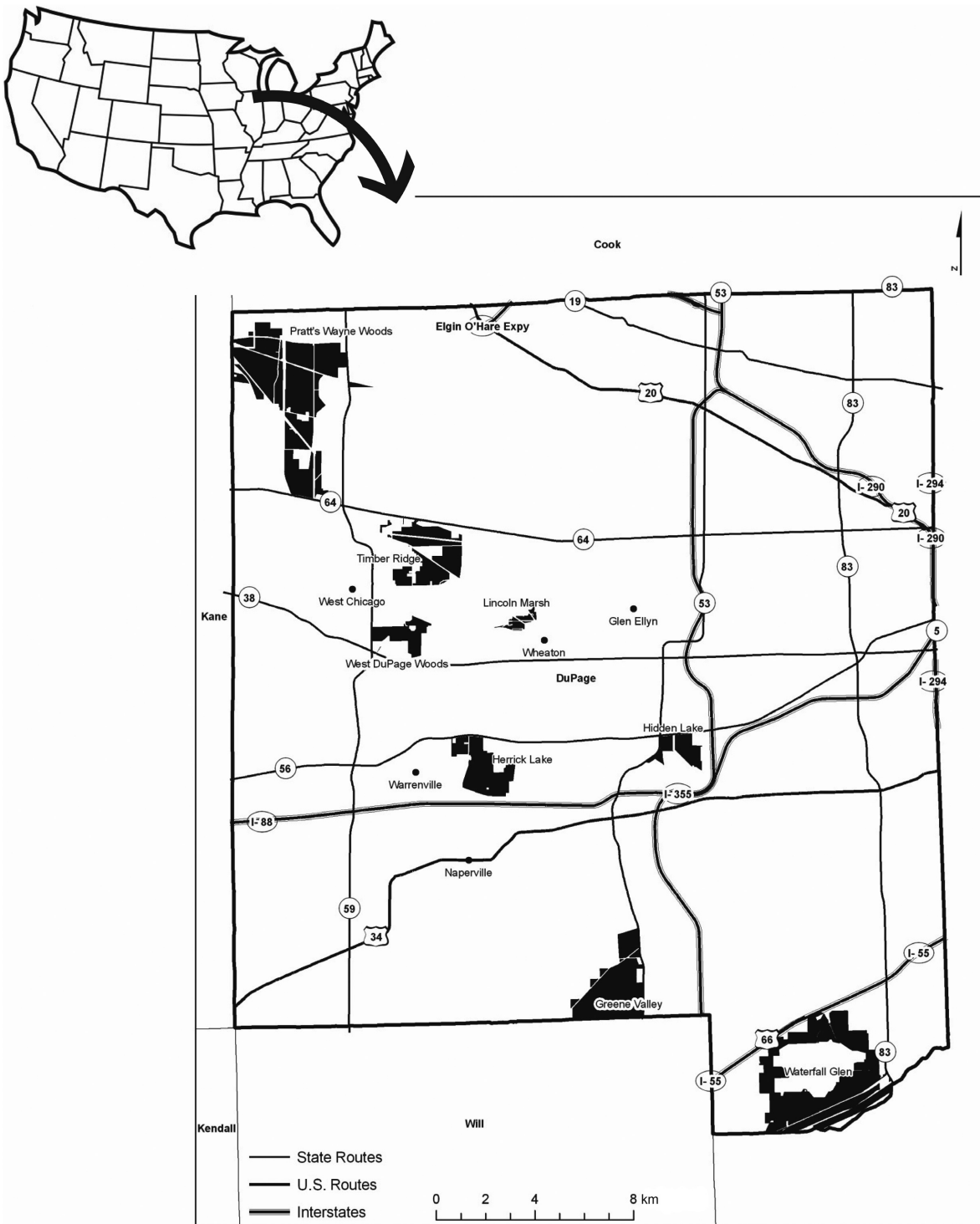


Fig. 1. Locations of forest preserves and associated marshes, clustered vernal pools, and isolated vernal pools used as study sites in DuPage County, Illinois (USA), 2008–2010.

up shortly after sampling began in 2008 and never refilled, and the other was discovered, in 2009, to be <100 m from a previously undetected pool, disqualifying it as an isolate. Thus, the final sampling array consisted of three isolated pools, six pool clusters ($X = 2.5$ pools/cluster), and six marshes.

Hydrology

Duration of water retention in amphibian breeding habitat, especially forest pools, is considered the most important abiotic factor affecting community composition, population size, and breeding success of pool-breeding amphibians (Skelly et al. 1999, Snodgrass et al. 2000a, Baldwin et al. 2006a, Karraker and Gibbs 2009). Therefore, we selected pools and marshes that retained water throughout the breeding season of all amphibians in these communities in all years. From 11 May to 22 June 2010, the height of the breeding season for most anuran species in these communities, we determined depth at 0.5-m intervals along major and minor axes of each pool. Selected pools were similar in area, elliptical in shape, and parabolic in form.

We placed calibrated stakes at the deepest point in each pool and monitored changes in water depth twice per week. Combining data from changes in water depth with records of daily weather conditions from the nearest daily recording station at Saint Charles, IL, we determined estimates of daily evaporation rates. Although each pool had a unique hydrologic signature, none dried up during the study period. This was consistent with a predictive function we developed for changes in water levels based on daily weather records and derived calculations of precipitation, evapotranspiration, and evaporation using a simplified version of the Penman method (Penman 1948, Linacre 1977). We concluded that selected pools or clusters offered environments of sufficient duration to permit development of amphibian larvae and survival of adults.

Landscape matrix

We assessed two measures of the general habitat and disturbance matrix surrounding wetlands of each category (marsh, isolated, clustered): percent forested canopy and, as a measure of anthropogenic disturbance, mean percent impervious land cover (e.g., paved roads, concrete, parking

lots), two variables that disproportionately affect amphibian community composition and density in forested landscapes (Houlahan and Findlay 2003, Eigenbrod et al. 2008). We obtained the 2011 National Land Cover Dataset layers on mean percent forested canopy cover and mean percent impervious land cover, each at a resolution of 30 m across the entire study area (Xian et al. 2011, Homer et al. 2015). We then used a Geographic Information System to calculate the mean forested canopy cover and mean impervious cover within a 500-m radius of each wetland, encompassing an area other investigators have determined to reflect a plausible amphibian (particularly anuran) terrestrial habitat zone congruent with known adult migratory distances (Baldwin et al. 2006a) and of sufficient size to contain a “conservation core zone” for anurans (Semlitsch 2002). We used one-way ANOVAs to test for differences in landscape-level forested canopy cover and landscape-level impervious surface cover among wetland types.

Data analysis

Species richness, community structure, and diversity.—We treated amphibian species richness (number of different species present at each site) as a response variable in different wetland categories and years using repeated-measures ANOVA with wetland category designated as treatment effect and year as repeated measure. Community composition at each site in different categories was quantified using the Chao-Jaccard Index, an easily interpreted measure of association between communities, and data grouped by year and category. We recorded relative abundance for anurans as 1 (single individual calling), 2 (multiple but distinguishable individuals calling), or 3 (chorus of multiple individuals that could not be separately distinguished), using the maximum value recorded for each species at each site in a given year (Weir 2001).

The Chao-Jaccard Index should not be analyzed using standard analysis of variance because, like other association measures, it violates assumptions of analysis of variance techniques. To extend analysis of the Chao-Jaccard Index across multiple community comparisons, we analyzed composition of amphibian communities using the linear model proposed by Dyer (1978) based on a blocked (by site) permutation

test developed by Edgington (1995; implemented using Excel macro DISSIM.XLS). We also used this analysis to determine contributions of each species to relative similarity among wetland categories.

Effects of increased connectivity associated with clustered pools could be confounded by the increased breeding area they offer. The positive relationship between area and species richness has been long known (Darlington 1957) and well studied (Fangliang and Legendre 1996). Additionally, some studies of U.S. Midwest amphibians have indicated that breeding area had greater effect on amphibian populations than species dispersal distance (and, by inference, habitat connectivity; Rustigian et al. 2003). Accordingly, we evaluated the strength of relationship between pool area and species richness via linear regression without regard to category. We considered pool area for clusters to be the total pool area of all pools in the cluster because each cluster was treated, in all aspects of our analysis, as an independent sampling unit, whereas individual pools in the same cluster would not possess such independence. Additionally, pools in a given cluster were consistently similar in area, with differences between areas of the largest and smallest pools in the same cluster varying by only 0.02–0.07 ha. Species–area relationships are normally evaluated at log scales due to large differences in number of species and areas of sampling units, but, in our case, the range of both species numbers and site-specific breeding areas was so small that simple linear regression was a more appropriate analysis.

Amphibian abundance.—We used ordinal logistic regression (package “ordinal” in Program R, version 3.0.1, <https://www.r-project.org>) to evaluate whether relative abundance of each anuran species differed at isolated pools and marshes compared to clustered pools. We used simple logistic regression (Program R) to evaluate probability of salamander species at isolated pools and marshes compared to clustered pools. We recorded salamander species as 0 if absent or 1 if present (≥ 1 individual captured at the site in that year) to avoid inflating the value of the Chao-Jaccard Index and ensure that interpretation of abundance was conservative. In both regression analyses, we considered a P -value < 0.10 significant because of the relatively small sample size of site-years.

Species occupancy dynamics.—We modeled dynamics of occupancy at sample sites using the MacKenzie et al.’s (2003) approach in program PRESENCE (version 8.4, www.mbr-pwrc.usgs.gov/software/presence.html). We used simple multi-season models for each species, whereby each model consisted of different parameterizations of four variables of interest: initial occupancy (proportion of sites occupied at the beginning of the study), colonization (rate at which unoccupied sites become occupied between years), extinction (rate at which occupied sites become unoccupied between years), and detection probability (probability of detecting a species during a sampling event if it is present; MacKenzie et al. 2003). We calculated naïve detection rates as the proportion of sampling events with the species detected given that they were ever detected at that site.

We treated each year (2008–2010) as a sampling period and each survey as a sampling event. Because anurans are most detectable during their breeding season, and because the timeframe of the breeding season was different for each species, we restricted analysis for each species to its own breeding season. Thus, there were a different number of sampling events (range = 9–37) within each sample period across species.

The development of candidate models followed a simple rule structure to test hypotheses of interest while avoiding all-subset modeling (Burnham and Anderson 2002). We tested whether detection probability for a given species was constant or varied by wetland category (marsh, clustered pools, or isolated pool). We then tested whether baseline occupancy was constant or varied by wetland category, and whether colonization and extinction were constant, varied by category, or varied inter-annually without regard to category. Colonization and extinction parameters were specified in the same way in all candidate models (e.g., varied by wetland category). We evaluated seven initial models given these constraints, including a full null model (all variables were constant) to assess model fit. Based on results for best a priori models, we also sometimes added post hoc models that did not constrain colonization and extinction to the same specification. We used information-theoretic methods (Akaike’s Information Criteria [AIC]) to evaluate hypotheses based

Table 1. Probability of detecting a species on a single survey during its respective breeding season and over the course of the study in DuPage County Forest Preserves, Illinois (USA), 2008–2010.

Species	Beta (P)†	SE (Beta)	Model-based P for single survey‡	Naïve P for single survey	X number of surveys§	Probability of detection during study¶
Eastern tiger salamander	−1.315	0.090	0.212	0.149	67.4	1.000
American toad	−1.568	0.103	0.172	0.148	46.7	1.000
Cope's treefrog	−0.930	0.607	0.283	0.108	35.7	1.000
Gray treefrog	2.708	1.033	0.938	0.960	5.3	1.000
American bullfrog	0.662	0.215	0.660	0.464	17.9	1.000
Green frog	−0.184	0.122	0.454	0.368	35.9	1.000
Northern leopard frog	−1.243	0.249	0.224	0.214	16.0	0.983
Eastern newt	−0.669	0.128	0.339	0.188	67.4	1.000
Spring peeper	0.135	0.145	0.534	0.477	54.6	1.000
Western chorus frog	0.485	0.080	0.619	0.644	34.5	1.000

† Coefficient estimate for detection probability on the logit scale.

‡ Probability of detecting the species, given that it is present, during a single site visit/survey.

§ Average number of surveys conducted during each species breeding season over the course of the study (i.e., three years).

¶ Model-based probability of detecting a species during the study period, given that it was present, for the average number of surveys conducted at a site during each species breeding season (note: Assumes geographic closure among years—no local extinction/colonization).

on strength of evidence in support of each candidate model being the best among the set. When models were competing as top model (e.g., $\Delta AIC \leq \sim 2.0$), we present results from the simplest model (Burnham and Anderson 2002). We only present results from a single model for each species (either the top model or simplest competing model) and did not calculate model averages because of potential loss of accuracy of estimated parameters (Richards et al. 2011), parameter coefficients being equivalent among competing models, and our emphasis on hypothesis testing via competing candidate models and not strictly on parameter estimation.

RESULTS

Detection rates, species richness, and community structure

Naïve (single survey) detection rates varied from 0.11 (Cope's treefrog) to 0.96 (gray tree frog; Table 1). Given our intensity of sampling effort, the probability of detecting a species during the study was 1.00 (certainty) for every species except northern leopard frog (0.98; Table 1).

Isolated pools, pool clusters, and marshes contained eight species of anurans and two species of salamanders (Table 2; Appendix S1). Species richness was independent of year ($F_{2,12} = 0.19$, $P = 0.83$), but not wetland category ($F_{2,12} = 6.54$, $P = 0.01$). Isolated pools had less than half the

average species per site ($X = 1.89$, $SD = 0.78$) as marshes ($X = 4.22$, $SD = 1.31$) or clustered pools ($X = 4.13$, $SD = 1.06$). Only clustered pools contained all (10) local species, including 3, Cope's treefrog, eastern newt, and spring peeper, unique to clustered pools (Table 2).

Differences in community similarity reflected differences in composition of species assemblages. Communities showed a baseline similarity (similarity of different sites in the same category in the same year) of 0.52 (52% similarity). Wetland category and annual variations affected community

Table 2. Presence (P) and absence (A) of local amphibian species in isolated forest pools ($n = 3$), clustered forest pools ($n = 6$), and marshes ($n = 6$) in DuPage County Forest Preserves, Illinois (USA), 2008–2010.

Species	Isolated pools	Clustered pools	Marshes
Eastern tiger salamander	P (22)	P (53)	P (24)
American toad	P (22)	P (82)	P (83)
Cope's treefrog	A	P (6)	A
American bullfrog	A	P (35)	P (56)
Green frog	P (22)	P (53)	P (89)
Northern leopard frog	A	P (22)	P (44)
Eastern newt	A	P (17)	A
Spring peeper	A	P (17)	A
Western chorus frog	P (100)	P (100)	P (100)
Gray treefrog	A	P (6)	P (17)

Note: Values in parentheses are average percentages of sites occupied each year.

Table 3. Similarity of amphibian communities (Chao-Jaccard Index) associated with isolated vernal pools, clustered vernal pools, and marshes in DuPage County Forest Preserves, Illinois (USA), 2008–2010.

Comparison	Year			Combined years
	2008	2009	2010	
All categories	>0.01	0.01	0.08	>0.01
Clusters-Isolates	0.03	0.10	0.55	0.06
Marshes-Clusters	0.17	0.26	0.12	0.31
Marshes-Isolates	>0.01	0.01	0.24	0.01

Notes: Values represent probabilities that community compositions in different categories are not different. Total number of permutations for comparison of all sites = 10,000. Total number of permutations for comparison of marshes and pools = 5005. Total number of permutations for comparison of clustered vernal pools and isolated vernal pools = 84.

composition. Differences in wetland categories reduced similarity between sites in different categories in the same year by 38% (category site similarity in the same year = 0.32). Likewise, community composition of sites in the same category was affected by annual variation, reducing similarity between sites in the same category in different years by 31% (different year site similarity = 0.36). Overall amphibian community composition was dissimilar among categories in all years combined ($P < 0.01$) and in most years separately (Table 3). Species contributing most to site similarity were western chorus frog and American toad (Table 4), both of which were present at all sites in all categories in ≥ 1 year. Eastern newt, Cope's treefrog, gray treefrog, and spring peeper

Table 4. Relative contribution to similarity (%) of 10 species of amphibians found in DuPage County Forest Preserves, Illinois (USA), 2008–2010.

Species	Relative contribution to similarity (%)
Western chorus frog	30.61
American toad	22.74
Green frog	19.24
Eastern tiger salamander	10.50
American bullfrog	8.16
Northern leopard frog	6.12
Eastern newt	1.75
Cope's treefrog	0.87
Gray treefrog	0.87
Spring peeper	0.00

Note: Summed percent contribution does not equal 100.0% due to rounding error.

contributed least to community similarity, being specific to particular sites in individual categories. All but one of these (gray treefrog) occurred only in clustered pools, and none occurred in isolated pools. Pool area contributed little to community differences. Variation in area (range 0.11–1.43 ha) explained <2% of variation in species richness (range 2–7 species; $r^2 = 0.018$), and there was no relationship between richness and area ($F_8 = 0.13$, $P = 0.73$; Fig. 2).

Amphibian abundance

Anuran species that occurred in both isolated pools and clustered pools had higher relative abundance at clustered pools. The odds of an anuran species having higher relative abundance in an isolated pool was 0–0.22 times lower than that of the same species in clustered pools (Table 5). Most anuran species that occurred in both marshes and clustered pools had higher relative abundance in marshes. Gray treefrog, American toad, American bullfrog, green frog, and northern leopard frog were 2.12–6.61 times as likely to have higher relative abundance in marshes compared to clustered pools (Table 5). Eastern newts and eastern tiger salamanders were less likely to occur in either isolated pools or marshes than in clustered pools (Table 5).

Species occupancy dynamics

Five species had detection histories suitable for occupancy modeling: green frog, American toad, American bullfrog, northern leopard frog, and tiger salamander. Spring peeper, Cope's treefrog, and eastern newts were found only at clustered pool sites, precluding estimation of category-specific occupancy parameters. Western chorus frog was precluded from occupancy modeling because they were found at nearly every site in every year (e.g., 100% site occupancy).

Four of the five modeled species showed evidence that detection probability was not constant and differed among wetland categories (ΔAIC range = 8.62–29.29, except 2.07 for northern leopard frog). For all but the eastern tiger salamander, detection probability was highest at marsh sites, lower at clustered pools, and lowest at isolated pools. American bullfrog and northern leopard frog were never detected at isolated pools. Tiger salamander detection probability was equivalent at clustered and isolated pools,

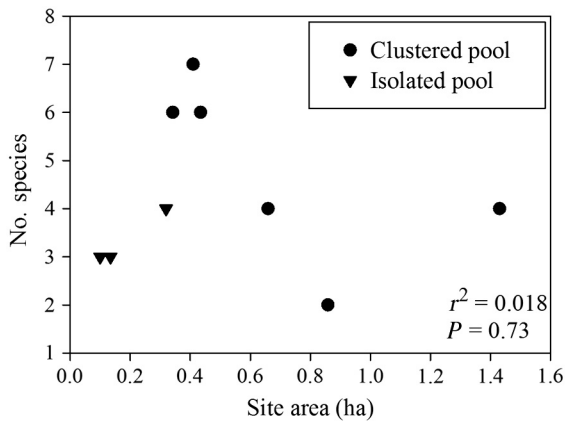


Fig. 2. Relationship of open-water area (ha) with amphibian species richness associated with three isolated pools and six groups of clustered pools in DuPage County Forest Preserves, DuPage County, Illinois (USA), 2008–2010.

but lower at marsh sites. The best models showed improvement over the quasi-null model (all parameters held constant except detection probability, which was allowed to vary by wetland category; ΔAIC range = 2.51–6.30) for all species except northern leopard frog (ΔAIC = 1.14; Table 6).

Effect of wetland category on occupancy parameters varied by species (Table 6). Only the

American bullfrog unequivocally showed a single best model among the candidate set, indicating that initial site occupancy differed among categories, colonization rates depended on year but not category, and extinction rate was constant across years and categories.

Landscape matrix

The forested and disturbed landscape matrix was not different among wetland types for percent impervious cover ($P = 0.840$), but percent forested canopy cover associated with marshes was lower than other wetland types ($P = 0.075$). Average percent impervious cover ($\pm\text{SD}$) was low and equivalent among all wetland types, 5.08% ($\pm 2.61\%$) for clustered pools, 4.05% ($\pm 2.54\%$) for isolated pools, and 6.25% ($\pm 7.77\%$) for marshes. Average percent forested canopy cover was 55.17% ($\pm 6.16\%$) for clustered pools, was 46.31% ($\pm 7.31\%$) for isolated pools, and was 38.52% ($\pm 15.76\%$) for marshes. One marsh had noticeably higher surrounding impervious land cover (18.1%) and another uncharacteristically low surrounding forested canopy cover (16.1%). If each outlier marsh was removed from calculations, marsh landscapes were similar to isolated pool landscapes (mean \pm SD) for impervious cover ($3.87\% \pm 5.76\%$) and forested canopy cover ($43.01\% \pm 12.63\%$).

Table 5. Differences in relative abundance (anurans) and presence/absence (salamanders) at isolated pools and marshes compared to clustered pools.

Species	Analysis	Isolated pools			Marshes		
		Odds ratio	95% Wald C.I.	<i>P</i>	Odds ratio	95% Wald C.I.	<i>P</i>
American toad	O	0.22†	0.05–1.02	0.052†	2.12	0.60–7.58	0.246
Cope's treefrog	O						
Gray treefrog	O				3.52	0.33–37.62	0.298
American bullfrog	O				3.54†	0.96–13.07	0.058†
Green frog	O	0.16†	0.03–0.99	0.048†	6.61†	1.71–25.58	0.006†
Northern leopard frog	O				2.85	0.68–11.93	0.152
Spring peeper	O						
Western chorus frog	O	0.20	0.02–2.60	0.219	0.16	0.02–1.58	0.117
Eastern tiger salamander	S	0.11†	0.01–1.09	0.060†	0.18†	0.04–0.85	0.030†
Eastern newt	S	0.00		0.996	0.19	0.02–1.92	0.160

Notes: Odds ratios <1 or >1 , respectively, indicate lower or higher abundance or probability of presence compared to clustered pools for each species. All species were observed ≥ 1 at clustered pools. Spring peeper (*Pseudacris crucifer*), and Cope's treefrog (*Hyla chrysoscelis*), models failed to converge because they were never detected in isolated pools or marshes. Gray treefrog (*Hyla versicolor*), northern leopard frog (*Lithobates pipiens*), and American bullfrog (*Lithobates catesbeianus*) were never detected in isolated pools, and this wetland category was excluded from the model to achieve convergence. Each species was modeled separately using either ordinal logistic regression (O) for relative abundance or a simple logistic regression (S) for presence/absence data. Traditional 95% confidence intervals are presented; due to the fairly low sample size, odds ratios significant at $\alpha = 0.10$ are noted.

† Significant at $\alpha = 0.10$.

Table 6. Model selection results for occupancy dynamics of green frog (GF), American bullfrog (AB), American toad (AT), northern leopard frog (NLF), and eastern tiger salamander (ETS) at breeding sites in DuPage County Forest Preserves, Illinois (USA), from 2008 to 2010.

Species	Model no.	K†	Model parameter			Δ AIC‡	AIC weight	Σ AIC weight§
			Initial Occ.	Colon.	Ext.			
GF	1	8	Habitat¶	•	•	0	0.263	0.681
	2	10	Habitat	Seasonal#	Seasonal	0.25	0.232	
	3	10	Habitat	Habitat	•	0.7	0.185	
AB	1	8	Habitat	Seasonal	•	0	0.795	0.952
	2	8	•	Seasonal	Seasonal	3.75	0.122	
	3	6	•	•	•	6.3	0.034	
AT	1	9	Habitat	Seasonal	•	0	0.436	0.897
	2	8	Habitat	•	•	0.21	0.393	
	3	10	Habitat	Habitat	•	3.71	0.068	
NLF	1	7	Habitat	•	•	0	0.393	0.750
	2	6	•	•	•	1.14	0.222	
	3	9	Habitat	•	Habitat	2.14	0.135	
ETS	1	7	•	•	Seasonal	0	0.350	0.795
	2	8	•	Seasonal	Seasonal	0.47	0.277	
	3	9	Habitat	•	Seasonal	1.46	0.169	

Notes: Model parameters of “•” indicate that initial occupancy (Initial Occ.), colonization (Colon.), or extinction (Ext.) was held constant across wetland category and years. Summed AIC weight for the top three models is included to highlight the cumulative information content of those models vs. those not presented here.

† Number of model parameters.

‡ Difference in Akaike’s information criteria (AIC) between each model and the model with the lowest AIC value.

§ For top three models only.

¶ Model parameter estimated separately for each wetland category.

Model parameter varied among years (i.e., sampling season).

|| Occupancy was fixed at zero for isolated pools for convergence (no individuals ever detected).

DISCUSSION

Fundamental questions

This study was designed to answer three questions. First, do clustered forest pools display greater amphibian species richness, abundance, and species occupancy rates than isolated forest pools? Second, as habitats for breeding amphibians, are forest pools complementary or redundant in their amphibian communities compared to marshes within the local landscape? Third, do species-specific probabilities of occupancy, colonization, and extinction differ by species and wetland type? Although our sample sizes, particularly in isolated pools, were small, the intensity of our sampling effort generated high detection probabilities of each species, such that we could verify that if a species was present at a site, it was detected during the study. Although we used appropriately different measures for estimation of abundance of anurans and salamanders, the Chao-Jaccard Index, our metric for estimation of community similarity, not only permits but is designed to accommodate both

presence/absence data (salamanders) and indices of relative abundance (anurans) and therefore can make accurate comparisons of community composition even when both types of data are included. Thus, we have confidence in our results and conclusions drawn from them.

Effects of clustering on species richness and community composition

Species composition of amphibian communities differed across wetland categories; patterns of anuran abundance and salamander occurrence were consistent in direction and magnitude. Overall trends showed higher anuran abundance in marshes and clustered pools than in isolated pools, and salamanders were more likely to occur at clustered pools than at other categories. Model estimates supported these trends, although some models failed to converge because some species were never present in isolated pools, preventing analysis and estimation necessary for convergence.

Clustered pools possessed greater species richness than isolated pools, a fact noted in other

studies (Lehtinen et al. 1999). Because of a larger sample size of clustered pools than isolated pools, lower species richness observed in isolated pools might be a result of sample size, not habitat clustering. Arguably, additional isolated pools might have contributed additional species. Granted that our inferences must show constraint given the limitations of our sample size, we nevertheless note that there were no hydrologic differences between isolated pools and clustered pools, little change in species composition in isolated pools over the three-year study period, and less change in community similarity attributable to annual variation than to categorical differences among these sampled sites. Pool clusters contributed, in the aggregate, more species than isolated pools or marshes. Further, anuran species present in both isolated and clustered pools were 100–500% more likely to have higher relative abundance in clustered pools. These considerations, in the aggregate, support the hypothesis that differences in species richness and composition of amphibian communities were most strongly influenced by breeding habitat arrangement, that is, clustering.

Such differences also cannot be explained by the surrounding landscape matrix, as different wetland categories showed similar levels of surrounding forest canopy cover and impervious surfaces (anthropogenic impacts). The first is a landscape variable known to have strong positive association with amphibian species richness and abundance, and the second a variable with disproportionate negative correlation with the same metrics (Houlahan and Findlay 2003, Eigenbrod et al. 2008). The differences in species richness, community composition, and odds of greater relative abundance that we recorded all suggested greater abundance and species richness existed in clustered pools than in isolated pools. Thus, differences in spatial configuration, connectivity, and proximity of habitat units were the most plausible causes.

Our study was not designed to evaluate recruitment, but we acknowledge that differences in recruitment in different wetland categories might also affect species composition, occupancy, colonization, and population persistence. Further examination of the effects of differences in recruitment on species composition in these and similar wetlands would provide valuable insights and a

more complete picture of key drivers of species composition in these communities.

Clustering and occupancy

When models are competing and nested, Burnham and Anderson (2002) recommended considering only the simplest model, as it provides the same amount of information with fewer parameters. We followed that recommendation. For five species with sufficient variation in occupancy rates to permit modeling, three had rates varying by wetland category (American bullfrog, American toad, and green frog), with rates highest at marshes (range 0.60–1.00), intermediate at clustered pools (range 0.11–0.60), and lowest at isolated pools (all rates effectively 0.0). Such differences suggest that marshes had higher abundance and occupancy rates for these three species, but clustered pools had higher abundance and occupancy rates than isolated pools.

It might be argued that clustered and isolated pools were not equivalent sampling units because greater breeding area associated with clusters contributed to greater species richness. In our study, species richness of clustered and isolated pools was independent of the area of open water in each pool or pool cluster, and therefore does not support this explanation, but rather confirms the conclusion of previous studies that wetland size should not be invoked as either the primary criterion for assessing wetland function or for amphibian species richness (Snodgrass et al. 2000a, Houlahan and Findlay 2003). Independent of size, some studies have demonstrated that species richness of pond-breeding amphibian communities varies with length of hydroperiod in fishless environments (Snodgrass et al. 2000b) and that hydroperiod may be the single most important abiotic factor structuring pool-dependent amphibian communities (Semlitsch et al. 1996, Skelly et al. 1999, Colburn 2004, Baldwin et al. 2006a). Our investigation of hydroperiods, however, revealed no differences between clustered and isolated pools, and so provided no basis to invoke hydroperiod variation as an explanatory mechanism for differences in species richness.

Many amphibian species exhibit characteristic patterns of metapopulation dynamics characterized by frequent, local, and site-specific patterns of extinction and colonization (Sjogren-Gulve 1994, Semlitsch 2000, Joly et al. 2001, Houlahan and

Findlay 2003). Similarly, previous studies have established that, in many species, immigration rates increase and extinction rates decrease with proximity to neighboring breeding ponds (Houlahan and Findlay 2003), and breeding areas never occupied by a given species tend to be farthest from colonizing sources (Skelly et al. 1999), contributing to the observed correlation between amphibian species richness and distribution of specific species with wetland isolation (Sjogren 1991, Sjogren-Gulve 1994, Skelly et al. 1999). Thus, the variation we observed in species richness was likely a consequence of clustering, reflecting importance of connectivity in these fragmented landscapes where even relatively small distances between pools can impose behavioral and physiological obstacles to amphibian movement (Compton et al. 2007) or increase predation risk.

CONCLUSIONS

Although based on a limited number of wetlands, these results suggest that management strategies that conserve clusters of forest pools in preserves would be beneficial to local amphibian populations. It might be prudent for managers to preserve a variety of representative wetland habitat types in any landscape wherever possible, these results indicate that managers should give priority to clustered pools over isolated pools if amphibian biodiversity is their objective, and when such prioritization is necessary due to limited resources for amphibian conservation. This would be especially true for clusters of pools with long (>18-week) hydroperiods, a time span that would encompass the developmental period of most amphibians and the breeding periods of all resident species in this area, and support larger populations and more diverse community assemblages (Baldwin et al. 2006a). Although our results are based on a small number of sample sites, the recommendations we derive from them are consistent with those of other investigators who have encouraged consideration of habitat connectivity as a critical element in amphibian conservation (Semlitsch 2000, Baldwin et al. 2006a) because breeding areas structured as clusters of pools reduce risk of local extinction associated with isolated wetlands, especially given limited dispersal abilities of some forest-dwelling amphibians (Karraker and Gibbs 2009).

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