
Amphibian Breeding Distribution in an Urbanized Landscape

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Abstract: *Amphibians commonly use wetlands for breeding habitat, and given the concern about their ongoing global declines, the effects of urbanization on the breeding distribution of amphibians need to be quantified. Thus, we conducted a survey of the larval amphibian community in central Pennsylvania (U.S.A.) wetlands along an urbanization gradient. Wetlands in urban areas had less surrounding forest and wetlands and greater road density than rural wetlands. Urbanization was also associated with increases in hydroperiod (i.e., wetland permanency) and the presence of fish predators. Moreover, urban wetlands had lower larval amphibian species richness than rural wetlands. This decrease in richness was attributable to a decrease in occurrence of wood frogs (*Rana sylvatica*) and ambystomatid salamanders (*Ambystoma maculatum* and *A. jeffersonianum*) in urban sites. Wood frogs and ambystomatid salamanders were positively associated with the amount of forest surrounding sites and negatively associated with hydroperiod. As a result, we hypothesize that these species are sensitive to the effects of urban development. The remaining species in this study appear fairly resilient to the effects of urbanization. These data demonstrate the importance of quantifying both local and landscape attributes when describing the factors that limit the breeding distribution of amphibians. We recommend that to preserve amphibian biodiversity in urbanized landscapes, it is best to focus on regional diversity, which protects a variety of sites that encompass various hydroperiods, have adequate buffer habitat, and are connected by dispersal routes.*

Key Words: species richness, urbanized landscape, wetlands

Distribución de la Reproducción de Anfibios en un Paisaje Urbanizado

Resumen: *Los anfibios comúnmente utilizan humedales como hábitat de reproducción, y dada la preocupación por sus declinaciones globales, existe la necesidad de cuantificar los efectos de la urbanización sobre la distribución de la reproducción de anfibios. Por lo tanto, examinamos la comunidad larvaria de anfibios en humedales de Pennsylvania central (E. U. A.) a lo largo de un gradiente de urbanización. Los humedales en áreas urbanas tenían menos bosque y humedales en los alrededores y mayor densidad de caminos que los humedales rurales. La urbanización también se asoció con incrementos en el hidróperiodo (i. e permanencia del humedal) y con la presencia de peces depredadores. Más aun, los humedales urbanos tenían menor riqueza de especies de larvas de anfibios que los humedales rurales. Este decremento en riqueza se debió al decremento en la ocurrencia de ranas (*Rana sylvatica*) y de salamandras ambistómidas (*Ambystoma maculatum* y *A. jeffersonianum*) en sitios urbanos. Las ranas y salamandras ambistómidas se asociaron positivamente con la cantidad de bosque alrededor de los sitios y negativamente con el hidróperiodo. Como resultado, planteamos la hipótesis de que estas especies son sensibles a los efectos del desarrollo urbano. Las especies restantes en este estudio parecen medianamente resistentes a los efectos de la urbanización. Estos datos demuestran la importancia de cuantificar tanto los atributos locales como los del paisaje cuando se describen los factores que limitan la distribución de la reproducción de anfibios. Para preservar la biodiversidad de anfibios en paisajes urbanizados, recomendamos enfocar la diversidad regional, que protege a una variedad de sitios*

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que abarcan varios hidropedimentos, tienen hábitat amortiguador adecuado y están conectados por rutas de dispersión.

Palabras Clave: humedales, paisaje urbanizado, riqueza de especies

Introduction

Declines in the biodiversity of ecosystems have been linked to factors such as global climate change, the establishment of exotic species, the emergence of infectious diseases, and urban development (Chapin et al. 2000). Of these agents, urbanization is perhaps the most overt and widespread. Urban development primarily affects the species richness of ecosystems via the loss or fragmentation of habitat (McKinney 2002). Urbanization is also associated, however, with increased exposure to contaminants, eutrophication, alterations in hydrology, and changes in the geomorphology of the landscape (Ehrenfeld 2000; McKinney 2002). Therefore, the impacts of urbanization on species richness are closely tied to alterations in both the local- and landscape-level attributes of ecosystems.

Of the ecosystems influenced by urban development, wetlands appear particularly sensitive. As a result of human development (e.g., agriculture, industrialization, and urbanization), wetlands have been lost at levels exceeding 50% during the last 200 years (Dahl 1990). Specifically, urbanization has been linked to wetlands loss in nearly all surveyed watersheds and may be responsible for up to 58% of total wetland loss in the United States (Ehrenfeld 2000). In addition to the direct loss of habitat, urbanization can also influence wetlands via changes in the linkages of wetlands to surrounding watersheds, ultimately leading to alterations in parameters such as hydrology and water quality (Richter & Azous 1995).

Because amphibians utilize wetlands extensively for breeding, changes in the quality of wetlands have the potential to influence breeding distributions in this group. The loss of wetlands is directly associated with a decrease in the numbers of breeding populations, a factor that can influence populations on a local and regional scale (Semlitsch 2000). The value of a wetland as breeding habitat to amphibians, however, is also susceptible to changes in within-site factors (e.g., degradation in water quality) that can act as stressors, altering biotic interactions and species survival (Kiesecker et al. 2001; Kiesecker 2002). Therefore, understanding how urbanization influences wetlands at both the landscape and the local level is paramount to understanding the factors that determine the breeding distribution of amphibians along urbanization gradients.

To assess the impacts of urbanization on wetlands and on the breeding distribution of amphibians in wetlands, we quantified the landscape and within-site attributes of

wetlands and their larval amphibian community along an urbanization gradient in central Pennsylvania (U.S.A.). We focused on larval amphibians because they are fairly easy to sample and because they are an obvious indicator of breeding in a given wetland. Although other researchers have classified the amphibian community of wetlands in fragmented landscapes (e.g., Richter & Azous 1995; Hecnar & M'Closkey 1998; Knutson et al. 1999; Lehtinen et al. 1999), they focused on multiple life-history stages to assess patterns of presence and absence. Observing adults or juveniles at sites may not adequately represent breeding distribution because occasionally these stages may be found in sites they would not normally use to breed. Moreover, these researchers did not focus specifically on urbanization or were limited by a low number of urban sites and no specific a priori designation of what constituted an urban wetland. We grouped wetlands into the categories of urban, suburban, and rural based on local human population density. We used these data to address the following questions: (1) do wetlands differ in surrounding landscape and within-site factors along the designated urbanization gradient and (2) what are the best predictors for a given amphibian species breeding in these wetlands?

Methods

Site Selection

We categorized the wetlands we surveyed as urban, suburban, and rural, with State College, Pennsylvania, as the urban center (Fig. 1). All these sites were located within a 16-km radius of State College. Wetlands varied in subcategories but were all defined as palustrine according to the National Wetland Inventory (NWI) designation (Cowardin et al. 1979). We determined urbanization classes by overlaying population data from local townships for Centre County, Pennsylvania (Pennsylvania State Data Center, Middletown), on NWI maps. Population densities of at least 450 people/km² defined urban areas, densities of 50–103 people/km² defined suburban areas, and 19–27 people/km² defined rural areas. We selected sites at random from all the sites in these categories. Because of problems in gaining access to some sites and the premature drying of others, we were unable to survey an equal number of sites in each category. We surveyed 18 urban, 25 suburban, and 14 rural sites. The sites were sampled once in May and once in July 2001. These dates were

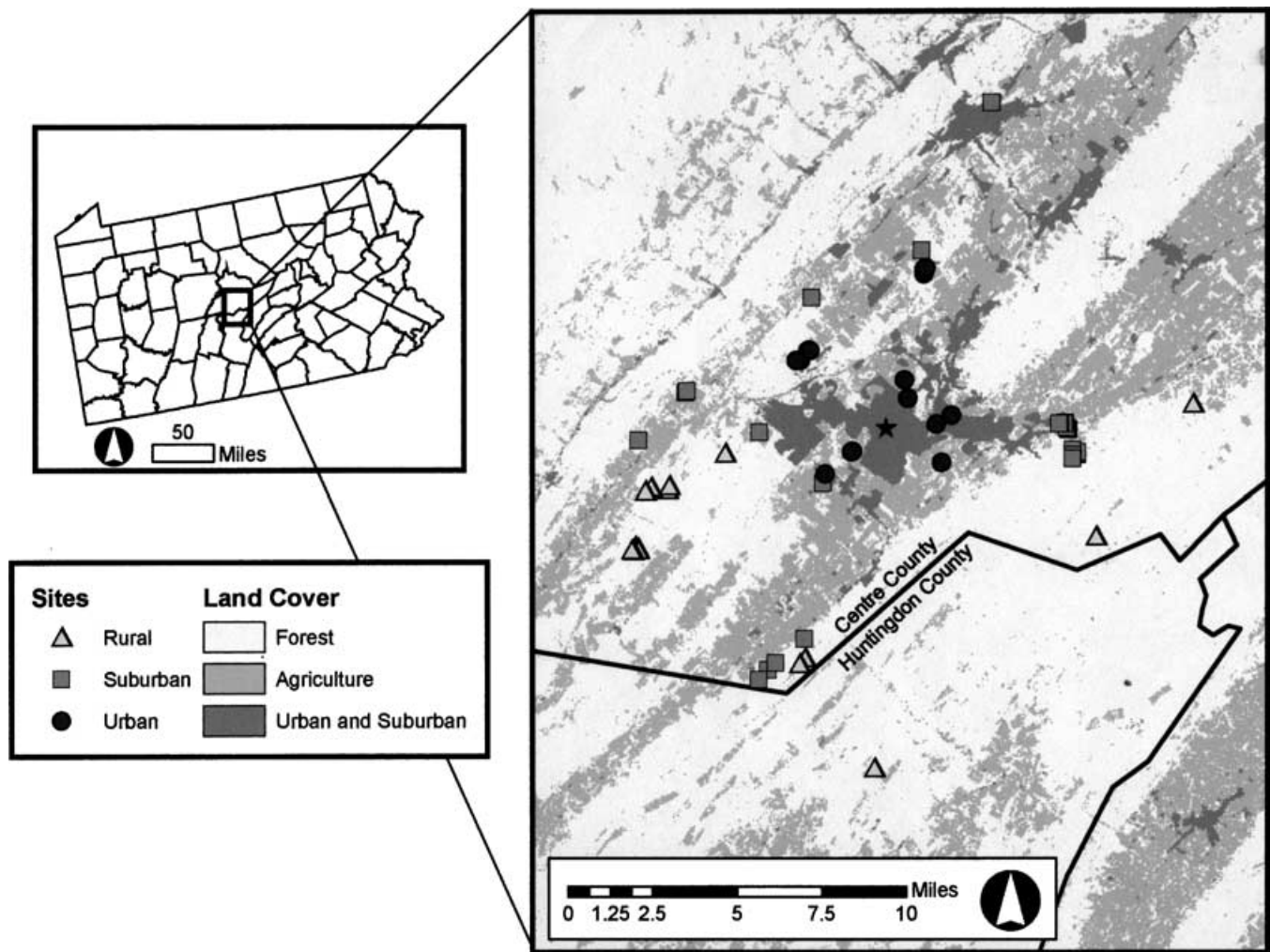


Figure 1. Location of the study sites in central Pennsylvania. State College (★) served as the urban center in this study.

selected to encompass the breeding periods of both spring- and summer-breeding amphibians.

Landscape Characteristics

We quantified landscape characteristics within a 1-km radius of each site. We chose this distance because it incorporates the dispersal capabilities of most pond-breeding amphibians that we encountered (Berven & Grudzien 1990; Semlitsch 1998). We used ArcGIS (version 8.3) and ArcView (version 3.2b; Environmental Systems Research Institute, Redlands, California) to assess landscape attributes. Percent forest was classified from Landsat TM (Thematic Mapper) data from the Pennsylvania Gap Analysis Program (The Penn State Institutes of the Environment, University Park). Road index was quantified using PAROADS (Pennsylvania Department of Transportation, Harrisburg). This program includes all road lines as depicted on U.S. topographic maps augmented by field study. In this program, the index increases as the length of

roads increases. We determined the number of wetlands (wetlands) within a 1-km radius and the distance to the nearest wetland (distance) with NWI maps.

Within-Site Characteristics

The area of each wetland was determined with the equation for an ellipse. We used a quantitative scale based on observations during sampling and previous experience at sites to determine the hydroperiod and the presence or absence of fish at each site. Permanent bodies of water received a 0, whereas wetlands that had dried were assigned a 1. Sites with fish present received a 1, and sites where fish were not observed or sampled received a 0. We quantified the percent canopy cover at sites with a densiometer. Readings were taken at the north, south, east, and west edge of the site and in the center. These values were then averaged to determine percent canopy cover. We measured pH and dissolved oxygen (DO) during daylight hours at the water's surface, approximately 1 m from

the shoreline, with handheld meters (Yellow Springs International, Yellow Springs, Ohio). We collected 250 mL of water from the surface of the site in acid-washed Nalgene bottles (Nalge Nunc International, Rochester, New York) and then froze the bottles immediately on returning to the laboratory. The samples were then analyzed for total nitrogen (TN) and total phosphorous (TP) at the Pennsylvania State University Agricultural Analytical Laboratory (methods followed Greenberg et al. 1999).

Amphibian Sampling

We used pipe sampling and time-constrained dip netting to sample amphibians. Pipes were 34 cm in diameter and approximately 1 m long. The number of pipe samples and the amount of time spent dip netting was determined by an a priori designation based on wetland size. This was done to ensure that our sampling effort was similar among sites. Small sites ($\leq 300 \text{ m}^2$) had 10 total pipes. Medium (approximately $300\text{--}1000 \text{ m}^2$) and large sites ($\geq 1000 \text{ m}^2$) had 20 and 40 pipes, respectively. To sample with a pipe, we selected an area haphazardly and thrust the pipe down into the substrate, forming a seal. We then removed the contents of the pipe by sweeping a net along the edge of the pipe, working from the bottom to the top. A single pipe sample was concluded when 10 consecutive sweeps were taken from the pipe without removing any animals. In addition to pipe sampling, we also used dip nets ($45 \times 35 \times 23 \text{ cm}$) to sample amphibians. The number of minutes spent dip netting equaled the total number of pipe samples (i.e., 10 pipes = 10 minutes of dip netting). If a species was captured at a site in low numbers (e.g., < 10 individuals), we used target sampling to obtain a larger number of individuals. Target sampling consisted of dip netting for an additional 15 minutes throughout the site. Moreover, if the site possessed a significant amount of open water ($> 50 \text{ m}^2$), we conducted five sweeps with a seine ($2.0 \times 7.5 \text{ m}$) in open water. All amphibians captured were preserved in 70% ethanol. The use of multiple techniques to sample larval amphibians helped to ensure that our sampling protocol adequately quantified these organisms. Based on our knowledge of these sites and the habitat requirements of local amphibians, we are confident that these sites were sufficiently sampled.

Amphibians were identified to species. Larval American toads (*Bufo americanus*) and larval Fowler's toads (*Bufo woodhouseii fowleri*) were grouped under the category *Bufo*, and larval spotted salamanders (*Ambystoma maculatum*) and Jefferson's salamanders (*A. jeffersonianum*) were grouped under *Ambystoma* because it was difficult to distinguish these species.

Statistical Analysis

We used multivariate analysis of variance (MANOVA) to compare landscape attributes and within-site characteristics among wetland classes. When MANOVAs were signif-

icant ($p < 0.05$), we conducted univariate analysis of variance (ANOVA) to test individual response variables. This "protected" approach to ANOVA guards against inflations in family-wise Type I errors (Scheiner 1993). We then used Tukey's tests to compare treatment means when significant differences ($p < 0.05$) were found with ANOVA. We also used ANOVA to examine amphibian species richness among wetland categories. Data were transformed, when appropriate, to conform to the assumptions of parametric statistics. We used chi-square analysis to examine the relationship between wetland class and the categorical variables of amphibian species presence/absence, hydroperiod, and fish presence/absence.

Because our landscape and within-site parameters were a mixture of categorical and continuous variables, we used stepwise logistic regression with a backward elimination procedure to determine what variables were the best predictors of larval amphibian species richness and the presence of each amphibian species in the surveyed wetlands. To develop a binary response for species richness, we divided sites into the categories of low (0) or high (1) species richness. Sites with two or fewer species were designated low richness, and sites with three or more species were designated high richness. Because we had no sites with more than five species, this allowed an equal number of levels in each richness category. To ensure an independent set of predictor variables, we used correlation analysis to determine which variables were highly correlated. We defined variables as highly correlated if the correlation coefficient was > 0.6 (Guerry & Hunter 2002). When pairs of variables were related, we removed the variable that was correlated with the greatest number of remaining predictors. We used a significance level of $\alpha = 0.05$ for inclusion into the models. We then assessed the fit of the models with the Hosmer-Lemeshow (H-L) statistic. According to the H-L statistic, a good model produces a nonsignificant result (Tabachnick & Fidell 2001).

Results

Wetland classes differed in terms of the measured landscape variables (Wilk's lambda: 9.50, $df = 8, 102$, $p < 0.001$). Percent forest and the number of wetlands within 1 km were significantly higher in rural sites than in urban or suburban sites (Table 1). Road index was lowest in rural sites; urban and suburban sites did not differ in terms of this factor. The distance to the nearest wetland was lowest in rural sites, highest in urban sites, and intermediate in suburban sites (Table 1).

Within-site factors also differed among wetland types (Wilk's lambda: 13.40, $df = 10, 100$, $p < 0.001$). The area of wetlands and pH were lowest in rural sites but did not differ between urban or suburban sites (Table 1). Percent canopy cover was highest in rural sites, whereas

Table 1. Summary of mean values and standard errors (SE) of amphibian species richness and landscape and within-site variables of wetland classes.

| Parameter | Wetland class ^a | | | p ^b |
|----------------------------|----------------------------|-----------------|---------------|----------------|
| | urban (SE) | suburban (SE) | rural (SE) | |
| Amphibian species richness | 1.61 (0.32)A | 2.36 (0.31)AB | 3.00 (0.36)B | 0.028 |
| Landscape variables | | | | |
| % forest ^c | 38.00 (5.99)A | 43.23 (4.97)A | 86.11 (2.05)B | <0.001 |
| wetlands | 7.06 (1.03)A | 8.80 (1.12)A | 15.71 (1.83)B | 0.007 |
| distance | 220.30 (65.7)A | 222.60 (80.1)AB | 48.50 (20.4)B | 0.055 |
| road index | 23.68 (3.37)A | 16.82 (2.08)A | 3.90 (1.54)B | <0.001 |
| Within-site variables | | | | |
| area (m ²) | 1818.00 (409)A | 2253.00 (502)A | 83.00 (398)B | 0.010 |
| % cover ^d | 17.11 (5.29)A | 19.56 (4.25)A | 70.04 (7.83)B | <0.001 |
| pH | 8.36 (0.23)A | 7.98 (0.14)A | 5.71 (0.26)B | <0.001 |
| DO ^e (mg/L) | 33.40 (14.0)A | 10.27 (1.54)A | 4.39 (0.99)B | 0.007 |
| TN ^f (mg/L) | 3.31 (0.51)A | 1.38 (0.25)B | 2.45 (0.27)A | <0.001 |
| TP ^g (mg/L) | 0.54 (0.18)A | 0.09 (0.02)B | 0.30 (0.09)AB | 0.005 |

^aUppercase letters represent comparisons of means based on Tukey's tests. Different letters indicate statistically significant ($p < 0.05$) differences.

^bValues based on a one-way analysis of variance of the specific parameter with wetland class as the independent variable.

^cPercent forest within a 1-km radius of sites.

^dPercent canopy cover over wetland.

^eDissolved oxygen.

^fTotal nitrogen.

^gTotal phosphorous.

urban and suburban wetlands did not differ in percent cover. Dissolved oxygen was highest in urban wetlands and lowest in rural wetlands, with suburban sites having intermediate values (Table 1). Total nitrogen was lowest in suburban wetlands but did not differ between rural and urban sites. Total phosphorous was highest in urban wetlands and lowest in suburban wetlands, with rural sites having intermediate values. Hydroperiod differed significantly among groups ($\chi^2 = 17.764$, $df = 4$, $p = 0.001$). Rural wetlands had shorter hydroperiods than either urban or suburban sites. The presence or absence of fish also differed between wetland classes ($\chi^2 = 17.164$, $df = 2$, $p < 0.0001$). Fish were more commonly observed in urban or suburban wetlands than in rural wetlands.

The species richness of amphibians differed significantly among wetland classes ($F_{2,54} = 3.83$, $p = 0.028$).

Richness was significantly higher in rural wetlands than in urban wetlands, with suburban sites having intermediate values (Table 1). We also found that wood frogs (*Rana sylvatica*) and ambystomatid salamanders (*A. maculatum* and *A. jeffersonianum*) were significantly more common in rural sites than in urban or suburban sites, whereas newts were significantly more common in both rural and suburban sites compared with urban sites (Table 2). The remaining species did not differ in their patterns of occurrence among wetland classes.

To determine what factors had the strongest associations with the presence of a given species, we first identified a set of independent predictor variables. Correlation analysis indicated that the variables of hydroperiod, area, percent forest, wetlands, distance, DO, and TP represented an independent set of predictor variables. These

Table 2. Proportion of sites occupied for each amphibian species among wetland classes.

| Species | Wetland class ^a | | | p ^b |
|--|----------------------------|---------------|------------|----------------|
| | urban (18) | suburban (25) | rural (14) | |
| Wood frog (<i>Rana sylvatica</i>) | 0.11 | 0.08 | 0.86 | <0.001 |
| Ambystoma (<i>A. maculatum</i> + <i>A. jeffersonianum</i>) | 0.11 | 0.04 | 0.86 | <0.001 |
| Eastern newt (<i>Notophthalmus viridescens</i>) | 0 | 0.28 | 0.36 | 0.026 |
| Bufo (<i>B. americanus</i> + <i>B. woodhousei</i> fowleri) | 0.44 | 0.48 | 0.14 | 0.096 |
| Spring peeper (<i>Pseudacris crucifer</i>) | 0.39 | 0.44 | 0.36 | 0.870 |
| Gray treefrog (<i>Hyla versicolor</i>) | 0.06 | 0.16 | 0.14 | 0.569 |
| Green frog (<i>R. clamitans</i>) | 0.28 | 0.44 | 0.14 | 0.146 |
| Bullfrog (<i>R. catesbeiana</i>) | 0.17 | 0.16 | 0 | 0.272 |
| Pickerel frog (<i>R. palustris</i>) | 0.06 | 0.28 | 0.07 | 0.082 |

^aNumber of sites in that class in parentheses.

^bValues are based on chi-square analysis of the frequency of occurrence for a species in each class.

Table 3. Stepwise logistic regression for larval amphibian species presence/absence in breeding sites in relation to the landscape and within-site attributes of wetlands.

| Factor ^a | Predictor(s) ^b | Sign | Estimate (SE) | t ratio | p ^c |
|---------------------|---------------------------|------|---------------|---------|----------------|
| Richness | % forest | + | 0.03 (0.01) | 2.35 | 0.019 |
| Wood frog | hydroperiod | — | 4.52 (1.30) | 3.45 | 0.001 |
| | % forest | + | 0.08 (0.03) | 2.52 | 0.012 |
| Ambystoma | hydroperiod | — | 2.78 (0.91) | 3.05 | 0.002 |
| | % forest | + | 0.06 (0.02) | 2.62 | 0.009 |
| Eastern newt | hydroperiod | + | 2.69 (1.18) | 2.29 | 0.022 |
| | % forest | + | 0.10 (0.04) | 2.53 | 0.011 |
| Pickerel frog | wetlands | — | 0.25 (0.10) | 2.63 | 0.009 |

^aSpecies not included in table were not significantly related to any predictor variables.

^bFull models included these variables: percent forest, wetlands, distance, hydroperiod, area, dissolved oxygen, and total phosphorous.

^cCriterion for inclusion into the model was $\alpha = 0.05$.

variables were included in the full models for species richness and the presence of each amphibian species. Larval amphibian species richness was positively associated with percent forest (Table 3). Wood frogs and ambystomatid salamanders were positively associated with percent forest and negatively associated with hydroperiod. Eastern newts (*Notophthalmus viridescens*) were positively associated with both percent forest and hydroperiod. Pickerel frogs (*R. palustris*) were negatively associated with wetlands (Table 3). We found no significant predictors for Bufo, spring peepers (*Pseudacris crucifer*), gray treefrogs (*Hyla versicolor*), green frogs (*R. clamitans*), or bullfrogs (*R. catesbeiana*). The models fit the data well ($p > 0.10$), suggesting that the models are reliable.

Discussion

Our results show alterations in the landscape and within-site attributes of wetlands across an urbanization gradient, and we observed differences in the larval amphibian community across this gradient. Generally, we observed fewer species in urban wetlands than in rural sites (Table 1). Declines in species richness in fragmented landscapes have been reported for amphibians in other locales (Richter & Azous 1995; Knutson et al. 1999; Lehtinen et al. 1999). The observed decrease in species richness is directly attributable to the rarity of ambystomatid salamanders and wood frogs in suburban and urban sites (Table 2). Therefore, we hypothesize that specific attributes of these species render them more susceptible to urbanization-induced habitat changes. The remaining species were frequently found in suburban or urban sites, or both, indicating that these species may be more resilient to urban development.

The absence of ambystomatid salamanders, wood frogs, and eastern newts in urban wetlands appears to be associated with a loss of forested habitat surrounding the

sites. These species were all positively associated with the amount of forested habitat that surrounded the sites (Table 3). Results of previous research have shown that these species are vulnerable to decreases in forested habitat (Gibbs 1998; Hecnar & M'Closkey 1998; Guerry & Hunter 2002). Because these amphibians have life-history stages that require forested habitat adjacent to breeding sites (Semlitsch 1998), decreases in the amount of forested habitat surrounding breeding sites may influence distributions by eliminating suitable postmetamorphic habitats.

Spring peepers, toads, and gray treefrogs also depend extensively on upland habitat. Toads, however, are considered habitat generalists (Hecnar & M'Closkey 1997), and spring peepers appear to be fairly insensitive to losses of forest habitat (Gibbs 1998). Thus, these species may be more resilient to the changes in the landscape resulting from urban development. It is not clear why gray treefrogs did not exhibit a response to urban development. This species was found at fairly low frequencies in all wetland classes (Table 2); therefore, the lack of a response may be confounded with low sample size. The postmetamorphic stages of the remaining species (i.e., green frogs, bullfrogs, and pickerel frogs) are primarily associated with aquatic habitats (Hecnar & M'Closkey 1998) and therefore may not be as vulnerable to a decrease in forested area surrounding breeding sites.

As the percentage of forest surrounding sites decreased, the number of wetlands decreased and the distance to the nearest wetland and the road index increased (Table 1). The presence of several wetlands in a landscape provides alternate breeding sites for amphibians (Skelly et al. 1999; Marsh & Trenham 2000). In a metapopulation context the availability of alternate breeding sites can stabilize regional populations if conditions at local sites become unfavorable for breeding. Thus, it is not clear why pickerel frogs exhibited a negative association with the number of wetlands surrounding sites. Further work is required to assess the relationship between the breeding of pickerel frogs and the presence of alternate breeding sites.

The increase in road index and distance between sites may also influence metapopulation dynamics by introducing barriers to dispersal. Although most amphibians can migrate large distances between breeding sites (Marsh & Trenham 2000), it is not clear how habitat fragmentation influences dispersal. deMaynadier and Hunter (1999) found that the emigration patterns of wood frogs and spotted salamanders were negatively affected by a decrease in forest canopy closure. Moreover, road density can also be a barrier to dispersal in wood frogs (Findlay et al. 2001). Therefore, we hypothesize that factors that limit the dispersal of amphibians (i.e., fragmentation of dispersal routes, increased distance between sites, and road density) also affect the breeding distribution of these amphibians by eliminating or reducing the flow of individuals between populations, thereby disrupting source-sink dynamics.

In addition to landscape factors, the within-site parameter of hydroperiod also influenced the breeding efforts of amphibians (Table 3). Hydroperiod is commonly believed to be a primary driver of the larval amphibian community composition in rural or undisturbed wetlands (Wellborn et al. 1996; Semlitsch 2000). We found that hydroperiod increased along the urbanization gradient. Most urban and suburban wetlands tended to be permanent. Urbanized wetlands commonly have modified hydrologic regimes (Ehrenfeld 2000), leading to a permanence of standing water. In accordance with an increase in the frequency of permanent water, there was an increase in the presence of fish—which are common predators of amphibians—in suburban and urban sites.

Previous researchers have found strong negative associations between fish presence and amphibian species richness (Hecnar & M'Closkey 1996, 1998). We believe that hydroperiod and the presence of fish played an important role in determining the distribution of amphibians in our study as well. In suburban wetlands, species such as bullfrogs and toads, which are unpalatable to fish predators (Kats et al. 1988; Hecnar & M'Closkey 1996), were common. Green frogs and spring peepers, however, which are palatable to fish (Kats et al. 1988; Werner & McPeck 1994), were also common across the urbanization gradient. These species may be capable of persisting in wetlands containing fish through behavioral adaptations that render them less susceptible to predation (Werner & McPeck 1994; Skelly 1996). Conversely, ambystomatid salamanders and wood frogs were rarely found in urban wetlands. These species appear to be particularly vulnerable to fish predation, with ambystomatid salamanders typically absent from ponds containing fish (Hecnar & M'Closkey 1996). In contrast, newts were positively associated with hydroperiod (Table 3). We believe that this may be the result of later breeding times of newts. Newts typically breed in late spring or early summer (Petranka 1998); therefore, they are frequently excluded from short-hydroperiod ponds because their larvae cannot metamor-

phose before the ponds dry. Because newts are also vulnerable to fish predation (Hecnar & M'Closkey 1996), the cost of breeding in short-hydroperiod ponds may outweigh the cost of predation by fish. These data suggest that hydroperiod may also play a significant role in determining amphibian distributions across urbanization gradients.

Conservation Implications

Our study shows the importance of quantifying the factors that determine the distributions of amphibians at multiple spatial scales. It appears that species are differentially affected by changes in the landscape and by changes in within-site factors of breeding sites along our urbanization gradient. Researchers differ in their evaluation of the importance of landscape versus local factors to amphibians. Beebee (1985) found that landscape variables were better predictors than within-site variables, whereas Knutson et al. (1999) found that landscape variables alone were limited in their effectiveness in describing their data sets. Because the species in our study responded to both landscape and within-site factors, it appears that studies at multiple spatial scales are required to effectively assess the factors that limit the distributions of amphibians in fragmented landscapes. We believe that these results apply to urbanization and to any disturbance that can affect ecosystems in both a landscape and a local context (e.g., Knutson et al. 1999; Lowe & Bolger 2002).

As a result of the patterns we observed, we hypothesize that ambystomatid salamanders and wood frogs are particularly sensitive to the effects of urban development and that the remaining species are more resilient to urbanization. To maintain breeding populations, sensitive species such as wood frogs and ambystomatid salamanders appear to require continuous forested upland habitat and fish-free wetlands. Resilient species such as newts, toads, spring peepers, gray treefrogs, green frogs, pickerel frogs, and bullfrogs appear to be able to tolerate a certain degree of disturbance as indicated by their presence in sites exposed to urban development. Preserving a diverse breeding community of amphibians in urbanized areas will be a daunting task because the nature of specific species' response to development likely depends on complex interactions among landscape, local, and biotic factors. Achieving a regionally diverse amphibian community in urbanized landscapes will depend on preservation of a variety of wetlands types, with surrounding buffer habitat of varying hydroperiods connected by dispersal corridors.

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