HABITAT AND LANDSCAPE CHARACTERISTICS UNDERLYING ANURAN COMMUNITY STRUCTURE ALONG AN URBAN–RURAL GRADIENT

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Abstract. Urbanization has been cited as an important factor in worldwide amphibian declines, and although recent work has illustrated the important influence of broad-scale ecological patterns and processes on amphibian populations, little is known about the factors structuring amphibian communities in urban landscapes. We therefore examined amphibian community responses to wetland habitat availability and landscape characteristics along an urban–rural gradient in central Iowa, USA, a region experiencing rapid suburban growth. We conducted call surveys at 61 wetlands to estimate anuran calling activity, and quantified wetland habitat structure and landscape context. We used canonical correspondence analysis (CCA) to examine patterns in anuran community structure and identify the most important variables associated with those patterns. Urban density at the landscape scale had a significant negative influence on overall anuran abundance and diversity. While every species exhibited a decrease in abundance with increasing urban density, this pattern was especially pronounced for species requiring post-breeding upland habitats. Anurans most affected by urbanization were those associated with short hydroperiods, early breeding activity, and substantial upland habitat use. We suggest that broad-scale landscape fragmentation is an important factor underlying anuran community structure in this region, possibly due to limitations on the accessibility of otherwise suitable habitat in fragmented urban landscapes. This study underscores the importance of a regional approach to amphibian conservation in urban and urbanizing areas; in fragmented landscapes, a network of interconnected wetland and upland habitats may be more likely to support a successful, diverse anuran community than will isolated sites.

Key words: amphibian; anuran; canonical correspondence analysis; community structure; connectivity; fragmentation; landscape; ordination; spatial scale; upland; urbanization; wetland.

INTRODUCTION

Urbanization is the primary cause of species endangerment in the contiguous United States (Czech et al. 2000) and has been shown to be a substantial component of amphibian population declines (Houlahan et al. 2000, Stuart et al. 2004). The effect of urbanization on pond-breeding anurans may be especially acute because many species require different breeding, nonbreeding, and hibernation habitats during their life cycle (Pope et al. 2000, Semlitsch and Bodie 2003, Cushman 2006). Urban development can therefore have a deleterious effect on anuran populations at multiple spatial scales. They are not only susceptible to the impairment of water quality and surface hydrology that tend to accompany urbanization (Pechmann et al. 1989, Vershinin and Tereshin 1999, Babbitt and Tanner 2000), but also to broad-scale landscape alteration and the resulting habitat fragmentation and loss of connectivity (Lehtinen et al. 1999, Houlahan and Findlay 2003, Rothermel 2004).

The loss of habitat connectivity that results from increased urbanization may also limit anurans' use of remnant habitat. Amphibians have demonstrated sensitivity to habitat contiguity and the presence of dispersal barriers (Hager 1998, Vos and Chardon 1998, Semlitsch and Bodie 2003, Trenham and Shaffer 2005), and Rothermel (2004) suggests that even small barriers can prevent successful juvenile emigration, due to the fine scale of landscape perception by amphibians. This underscores the challenges posed by urban landscapes, which are defined by a high degree of fragmentation, and thus, a high incidence of barriers to dispersal (McKinney 2002, 2006). It is possible, then, that urbanization limits the availability of anuran habitat in the landscape; otherwise suitable habitat embedded in an uninhabitable matrix is functionally unavailable to dispersing juveniles and migrating adults.

Fragmented urban landscapes likely restrict dispersal and migration, putting populations already subject to frequent localized extinction and colonization events at risk of extinction (Hecnar and M'Closkey 1996, Skelly et al. 1999, Marsh 2001, Marsh and Trenham 2001). Because anurans live only a few years at most (Lannoo 1998), the ability of juveniles to disperse readily through the matrix among breeding sites is critical to a

population's long-term survival (Stevens et al. 2004, Rothermel and Semlitsch 2002, Rothermel 2004).

The persistence of anuran populations in urban landscapes, therefore, may be influenced by a complement of factors at different spatial scales from individual breeding sites to entire landscapes. This idea is supported by recent literature from a variety of ecosystems across several continents (e.g., Pellet et al. 2004a, b, Drinnan 2005, Rubbo and Kiesecker 2005). Although individual species' responses to urban wetland habitat and landscape context have been investigated, studies examining the patterns of anuran community structure in urban landscapes are notably absent from the literature.

Recent studies have described factors driving community structure in urban areas for other taxa using a variety of multivariate statistics, although these analytical tools have not yet been applied to anuran communities (e.g., Germaine and Wakeling 2001, Hennings and Edge 2003, Miller et al. 2003, 2004, Hogsden and Hutchinson 2004). The most common statistical approach in the amphibian literature is logistic regression, assessing the influence of urbanization on the presence of individual species. Community-level analyses are generally limited to using multiple regression to look at factors influencing species richness. The strength of a multivariate approach is in its ability to provide insight into the relative importance of factors at multiple scales, while simultaneously evaluating the response of all species in the community to those factors. This is notably different from univariate methods, which allow only indirect inference about community-level patterns.

Using a combination of univariate and multivariate methods, we examined the influence of wetland habitat availability and landscape context on anuran community structure along an urban–rural gradient in central Iowa, USA. We chose a gradient approach, rather than a categorical classification of land use (e.g., "urban" vs. "rural"), because it has the advantage of being able to quantify continuous differences in community structure in relation to landscape context, as well as critical thresholds in that relationship (McDonnell and Pickett 1990, Gibbs 1998, Miller et al. 2001, Homan et al. 2004, Drinnan 2005, Denoël and Ficetola 2007).

METHODS

Description of study area

Central Iowa is primarily dominated by row crop agriculture, but >50% of its population now lives in urban or suburban areas; sprawl has emerged as a major concern for the area surrounding the city of Des Moines (Office of Social and Economic Trend Analysis, Iowa State University, *available online*).[4] Historically, this region comprised tallgrass prairie and wooded riparian corridors, with temporary depressional wetlands and oxbow lakes serving as the primary habitat for breeding anurans. As a result of human settlement, fewer than 10% of Iowa's wetlands and 0.01% of its prairies remain intact (Dahl 1990, Sampson and Knopf 1994). Anuran breeding habitat in central Iowa is now limited to farm ponds, subdivision impoundments, and urban lakes, as well as rural roadside ditches and some remnant and restored prairie potholes.

With the exception of the bullfrog (*Rana catesbeiana*), populations of all native anurans in Iowa have been declining for at least the last half-century because of increased rates of habitat fragmentation and loss (Christiansen 1981, 1998, Lannoo et al. 1994). Of greatest conservation concern in central Iowa is the cricket frog (*Acris crepitans*), which has already experienced severe declines in the northern portion of its range (Hay 1998, Lannoo 1998). Iowa now marks the species' northernmost extent (Kane et al. 2004).

Study site selection

We selected 61 remnant, restored, and constructed wetlands throughout central Iowa for inclusion in this study (Fig. 1). Study sites encompassed a gradient of land use from rural areas to the urban core, and were located on both private and public land (Appendix A). Potential sites were identified on color-infrared (CIR) digital orthophotos produced in 2002 (Iowa Geographic Map Server, *available online*).[5] Final site selection was based on two criteria. First, sites had to be at least 2 km apart to ensure independence in landscape analyses. Second, sites were restricted to semi-permanent or permanent ponds, containing at least 50% open water. Urban wetlands tend to be of this type and inclusion of temporary wetlands or those dominated by emergent vegetation would reduce our ability to detect differences owing to landscape context. Selected sites were ground-truthed and evaluated for adherence to said criteria.

Call surveys

We conducted a series of call surveys from March through July 2005, to coincide with the breeding seasons of all Iowa anurans (Table 1). Call surveys provide a measure of abundance that can be compared among sites, and offer an efficient means for collecting data over a broad spatial extent. We used an anuran call index as follows: 0, no individuals of a given species heard; 1, one individual heard; 2, multiple individuals with no overlap in calls; 3, full chorus (Hemesath 1998, Mossman et al. 1998).

Sites were organized geographically into nine routes to expedite call surveys. We visited all sites on a given route during the same evening, although the order was changed between visits to minimize the confounding influence of time of day. We employed a modified version of the sampling protocol developed for the
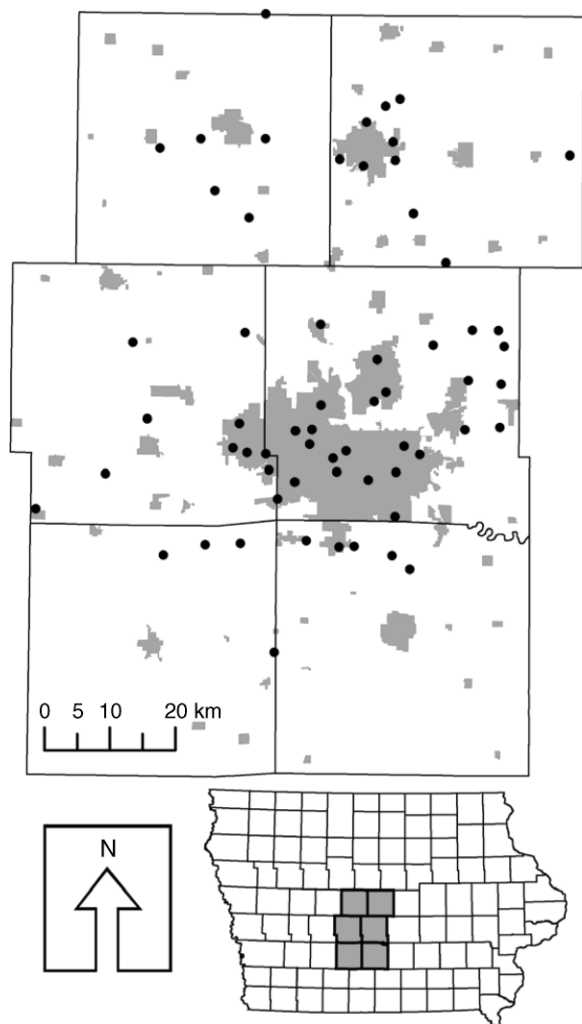
FIG. 1. Map of study area, showing 61 wetlands (black dots) in central Iowa, USA. Incorporated cities and towns are shown in gray.

North American Amphibian Monitoring Program (NAAMP; Weir and Mossman 2005). Whereas the NAAMP protocol calls for one 5-min survey at each site during three month-long sampling windows, we conducted 10-min surveys every two weeks to increase detection probability for rare or infrequently calling species (Bridges and Dorcas 2000, Crouch and Paton 2002). In accordance with NAAMP protocol, surveys were conducted at least 0.5 h after dusk and completed by 01:00, with air temperature >5.6°C, water temperature >10°C, and wind speed below 5.8 m/s.

Wetland habitat characteristics

We measured features related to habitat availability at the scale of the individual wetland using field sampling and a Geographic Information System (GIS; Appendix B). Water pH and conductivity were measured after every call survey using a handheld electronic meter (Oakton pH/Con 10, Oakton Instruments, Vernon Hills, Illinois, USA) at a depth of 5 cm, 1 m from the edge of standing water (Freda and Dunson 1985, Sjögren 1994). We also measured land cover in 10 randomly located 5 × 5 m plots along the perimeter of each wetland. Random sampling points were first established in GIS (ArcGIS 9, Environmental Systems Research Institute, Redlands, California, USA), and subsequently located on the ground using a Global Positioning System (GPS; Magellan Meridian, Thales Navigation, Santa Clara, California, USA). Each plot was arrayed along the wetland edge clockwise from the starting point. We defined the wetland edge as the furthest extent of hydric soils, as evidenced by the presence of wetland vegetation or other features indicative of long-term saturation. In addition to these metrics, we determined the presence or absence of fish, which has been shown to exert a strong influence on anuran abundance (e.g., Laurila and Aho 1997, Ficetola and De Bernardi 2004, Hazell et al. 2004, Porej and Hetherington 2005).

Wetland perimeter and the area of emergent vegetation were quantified in GIS using two sets of aerial photographs: CIR orthophotos taken during March 2002 and natural color orthophotos taken during August 2004 (Iowa Geographic Map Server; see

TABLE 1. Guild associations for seven central Iowa, USA, anuran species, based on peak breeding season and preferred habitat (modified from Knutson et al. [1999]).

Species	Breeding period	Habitat requirements		
		Breeding	Nonbreeding	Hibernation
Acris crepitans	June–July	perm. water	wetland	litter
Bufo americanus	April–May	temp. or perm.	upland	litter
Hyla chrysoscelis	April–May	temp. or perm.	upland	litter
Hyla versicolor	April–May	temp. or perm.	upland	litter
Pseudacris triseriata	April–May	temp. or perm.	upland	litter
Rana catesbeiana	June–July	perm. water	wetland	wetland
Rana pipiens	April–May	temp. or perm.	upland	wetland

Note: Descriptions of the terms are: Breeding, a species prefers to breed in permanent (perm.) ponds, or in either temporary (temp.) or permanent wetlands; Nonbreeding, a species is associated with wetland or upland habitats outside of the breeding season; and Hibernation, a species is known to hibernate in leaf litter or in mud under wetlands.

TABLE 2.   Component variables of the index of urban density, derived from the rotated PC1 scores of a principal components analysis (PCA).

Variable	Eigenvalue	Pearson r
Number of buildings/km^2 within 1 km of wetland	0.463	0.950
Percent cover of buildings within 1 km of wetland	0.463	0.951
Percent cover of roads within 1 km of wetland	0.439	0.920
Percent cover of lawn within 1 km of wetland	0.448	0.900
Number of wooded patches/km^2 within 1 km of wetland	0.422	0.865

Note: The eigenvalue is the weight given each variable, and Pearson r statistics refer to the correlation of each variable with the index of urban density.

footnote 5). Using these images from early spring and late summer allowed us to measure more accurately the temporal variation in spatial extent of saturation and wetland vegetation.

Landscape composition and configuration

We quantified landscape composition and configuration by digitizing land cover within 1 km of the wetland perimeter using natural color and CIR orthophotos (Appendix B). This distance is greater than the home range any of Iowa's anuran species, but smaller than the estimated dispersal distance of the two farthest traveling native species, *R. catesbeiana* and *R. pipiens*, offering a spatial extent encompassing landscape features relevant to both migration and dispersal (Knutson et al. 1999, Weir et al. 2005).

Univariate data analyses

We created an index of urban density using rotated PC1 scores from a principal components analysis (PCA; sensu Miller et al. 2003). The index was derived from five landscape metrics associated with the urban–rural gradient: building density, density of wooded patches, and the percent cover of buildings, roads, and lawns. PC1 explained 84.3% of the variance in the data, and showed high correlation with all five variables (Table 2). We scaled the raw PC site scores from 0 to 1, to increase interpretability (i.e., 0 = least urban, 1 = most urban).

To examine broad patterns of anuran diversity and abundance along the urban–rural gradient, we calculated two univariate response variables and regressed them against urban density: species richness (S_i) and total calling rank (C_i). Total calling rank is defined as

$$C_i = \sum_{j=1}^{S_i} \sum_{k=1}^{K_i} c_{ijk} \qquad (1)$$

where c_{ijk} is the call index value of species j at site i on occasion k, and K_i is the total number of sampling occasions at site i (modified from Pope et al. 2000). In other words, total calling rank is the sum of call values across all species at a given site. Although total calling rank is an imprecise measure of abundance, along with species richness it gives an indication of trends in the overall condition of the anuran community.

Multivariate data analyses

We used canonical correspondence analysis (CCA) to examine the relationship between anuran community structure and both wetland habitat availability and landscape context. CCA is a constrained ordination technique whose first axis is a linear combination of environmental variables that best explains variation in a matrix of species abundances (ter Braak 1986). Additional orthogonal axes explain the remaining variance in the community data. One strength of CCA is its ability to partition the amount of community variance explained by various subsets of the environmental data. We were therefore able to evaluate the relative importance of habitat availability and landscape structure by conducting a partial CCA on the habitat and landscape variables (Økland and Eilertsen 1994). Analyses were performed using the software packages PC-ORD 4.34 (McCune and Meffort 1999) and CANOCO 4.5 (ter Braak 2002).

To increase our ability to identify the important environmental factors underlying anuran community structure, we removed variables that covaried strongly ($|r| \geq 0.7$), retaining those with the most direct ecological interpretation. Environmental variables were transformed as necessary to achieve normality, using $\arcsin(x)$ for proportion data (e.g., percent cover of roads, percent cover of buildings) and $\ln(x+1)$ for other values (e.g., distance to nearest other wetland, mean area of herbaceous patches).

In the matrix of response variables (i.e., species), we used the calling rank of each species, defined as

$$c_{ij} = \sum_{k=1}^{K_i} c_{ijk} \qquad (2)$$

where c_{ijk} is the call index value of species j at site i on occasion k (sensu Pope et al. 2000). To counteract skewness, these data were transformed using $\ln(x+1)$. Because CCA requires at least one nonzero value per row (i.e., at least one species per site) in the community matrix to avoid dividing by zero, we omitted two sites containing zero species. CCA axis scores were standardized using Hill's (1979) method, which is thought to make the ordination more readily interpretable ecologically (McCune and Grace 2002).

TABLE 3. Variables used to quantify anuran breeding habitat and landscape context for 61 wetlands in central Iowa, USA.

				Intra-set correlation†	
Variable	Mean	SE	Range	Axis 1	Axis 2
Breeding habitat availability					
pH	8.3	0.06	7.1–9.3	0.451	0.005
Presence/absence of fish‡	—	—	—	0.238	−0.536
Wetland age§	—	—	—	−0.196	−0.554
Wetland perimeter (m)	711.5	63.1	132.7–2638.8	−0.177	−0.290
Area of emergent vegetation (ha)	0.51	0.19	0–11.2	−0.546	0.026
Percent cover of herbaceous vegetation within 5 m	52.4	4.6	0–100	−0.608	0.163
Percent cover of woody vegetation within 5 m	15.2	2.5	0–84.0	−0.110	−0.571
Landscape composition and configuration					
Distance (m) to the nearest other wetland‖	272.0	38.3	0–1000	0.168	0.268
Number of roads crossed to nearest other wetland	1.7	0.28	0–9	0.642	0.249
Mean herbaceous patch size (ha) within 1 km	6.3	2.5	0–132.2	−0.719	0.067
Mean wooded patch size (ha) within 1 km	1.3	0.27	0–8.6	−0.346	−0.056
Number of wetlands/km² within 1 km	3.1	0.47	0–19.2	0.001	−0.567
Percent cover of roads within 1 km	8.1	0.9	0.6–26.3	0.558	−0.069
Percent cover of herbaceous vegetation within 1 km	9.7	1.3	0–35.8	−0.630	0.071

Note: Dashes correspond to categorical or ordinal data, which have no mean or standard deviation.

† The correlation of a variable with each of the first two axes from canonical correspondence analysis (CCA). Axes 1 and 2 are the primary and secondary gradients underlying anuran community structure.

‡ Fish were recorded as present ($n = 23$ wetlands) or absent ($n = 38$ wetlands).

§ Wetland age was recorded using four ordinal categories: <3 years ($n = 3$), 3–10 years ($n = 17$), >10 years ($n = 35$), naturally occurring ($n = 6$).

‖ For sites with no other wetlands within 1 km ($n = 2$), distance was recorded as 1000 m.

In addition to quantifying species responses to the underlying environmental gradients, we identified potential mechanisms driving similar responses among different species. Species were organized into guilds based on life history traits to explore distributional patterns among species with similar breeding, nonbreeding, and hibernation habitat requirements. This approach gave insight into whether observed patterns of distribution were more likely explained by breeding season resource needs, summer upland habitat use, or overwintering success. While this was a qualitative approach, it allowed us to identify specific biological explanations for observed species distributions. We used the guilds defined by Knutson et al. (1999), because that study had a high degree of geographic overlap with our own.

RESULTS

Call surveys

We conducted call surveys on 58 nights, for a total of 339 site visits. Most sites were visited on six occasions, but some were visited only five times due to weather. To account for bias in our estimates, five visits to each site were chosen randomly and only data from those visits were included in analysis.

A total of nine species were observed, encompassing all but one species native to central Iowa: the cricket frog (*Acris crepitans*), American toad (*Bufo americanus*), Cope's and Eastern gray treefrogs (*Hyla chrysoscelis* and *H. versicolor*), chorus frog (*Pseudacris triseriata*), northern and Plains leopard frogs (*Rana pipiens* and *R. blairi*), and bullfrog (*R. catesbeiana*). Though the study area was within its recorded range, the green frog (*R. clamitans*) is very rare in central Iowa (Christiansen

and Bailey 1991) and was not detected. The study area marks the range boundary for two species recorded, *P. crucifer* and the *R. blairi*. We omitted these species from all analyses because we felt their rarity was more attributable to range extent than any measured environmental variables.

Habitat and landscape characteristics

The 61 study sites were aligned along the spectrum of land use from rural agricultural areas to Des Moines' urban core, with a somewhat higher proportion of sites located toward the rural end of the gradient. After excluding highly correlated variables, we retained 14 for analysis, divided evenly between breeding habitat and landscape metrics (Table 3). Most variables showed a negative correlation with urban density, with the exception of road density, wetland density, and the presence of barriers to dispersal (Fig. 2).

Overall influence of urbanization

There was a significant negative correlation between urban density and species richness ($r = -0.663$, $P < 0.0001$). Increased urban density also demonstrated a significant negative relationship with total calling rank ($r = -0.688$, $P < 0.0001$). Calling rank of all study species exhibited a negative relationship with urban density, although the decline of *R. catesbeiana* with increasing urban density was less pronounced than in other species (Fig. 3).

Environmental gradients underlying community structure

The linear combinations of habitat and landscape variables making up the first two CCA axes explained
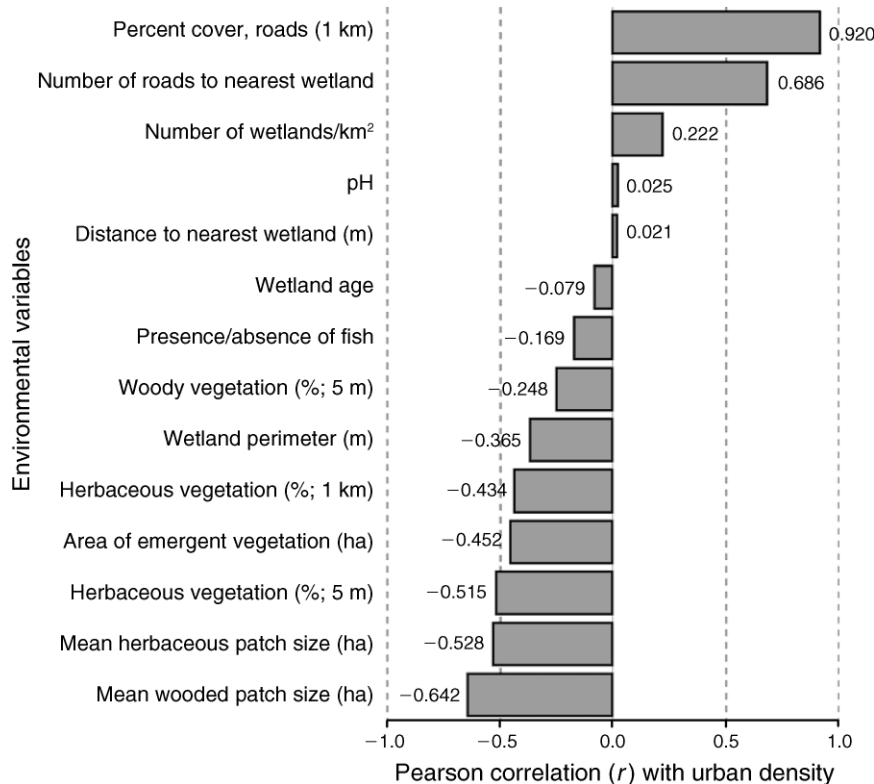
FIG. 2. Correlations between urban density (See *Methods: Univariate data analyses*) and all environmental variables. Distances within which data were collected are listed parenthetically. Wetland age was recorded using four ordinal categories: <3 years ($n = 3$), 3–10 years ($n = 17$), >10 years ($n = 35$), naturally occurring ($n = 6$).

24.9% of the community data variance. Partitioning the variance in a partial CCA showed that overall, landscape-scale factors explained somewhat more variance in the community data than did site-scale factors (19.8% and 16.2%, respectively).

We assessed the importance of component variables using their intra-set correlations (i.e., correlations between the ordinated axes and their component variables) rather than their raw canonical coefficients, because they provide a more accurate representation of the environmental gradients underlying community structure (ter Braak 1986). Axis 1 explained 13.8% of the variance in the community data. Five variables were most strongly correlated with axis 1: the number of road crossings to the nearest other wetland ($r = 0.642$), the percent cover of roads within 1 km ($r = 0.558$), the mean area of herbaceous patches within 1 km ($r = -0.719$), and the percent cover of herbaceous vegetation within 1 km ($r = -0.630$) and 5 m ($r = -0.608$). Axis 2, which explained an additional 11.1% of the community variance, correlated most strongly with three variables: the percent cover of woody vegetation within 5 m ($r = -0.571$), the patch density of wetlands within 1 km ($r = -0.567$), and wetland age ($r = -0.554$).

The first axis correlated strongly with the index of urban density ($r = 0.730$), indicating that the primary environmental gradient underlying anuran community structure was an urban fragmentation gradient. This was further reinforced by the location of study sites in the ordination space created by the first two axes in CCA (Fig. 4). Rural sites were more closely associated with more negative Axis 1 values, and urban sites tended to be arrayed at higher values.

Anuran community responses to underlying environmental gradients

Species showed some clustering within the environmental space created by the first two axes (Fig. 5). The relative abundance of *R. pipiens* and *H. chrysoscelis* was associated with negative axis 1 scores, indicating a strong positive association with abundant, unfragmented herbaceous vegetation at both the wetland and landscape scales, and a negative association with road density in the surrounding landscape. *Hyla versicolor* showed a more negative relationship with axis 2 than did other species, indicating higher relative abundance in clustered, longer established wetlands surrounded by woody vegetation. *Bufo americanus*, *P. triseriata*, and *A. crepitans* showed weaker associations with both axes than did other species. In contrast to most other study species, *A. crepitans* exhibited a relationship with slightly positive values along axis 1, perhaps attributable to a shallower decline in calling activity relative to most other species at moderately urban wetlands (Fig. 3a).
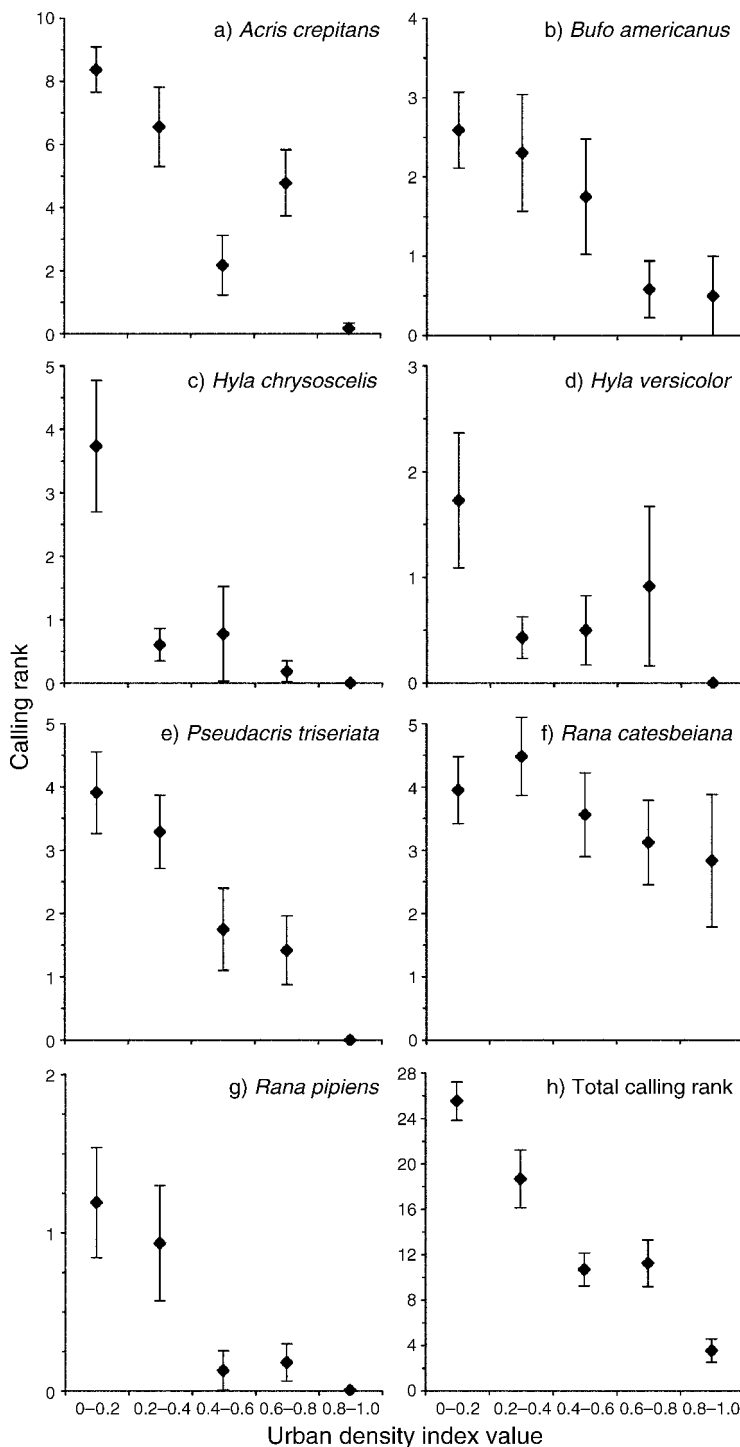
FIG. 3. Calling rank (mean ± SE; Eq. 1) of seven anuran species in equal quantiles of the index of urban density (0 = least urban, 1 = most urban; see *Methods: Univariate data analyses*): 0.0–0.2 ($n = 22$ sites), 0.2–0.4 ($n = 13$ sites), 0.4–0.6 ($n = 8$ sites), 0.6–0.8 ($n = 12$ sites), and 0.8–1.0 ($n = 6$ sites).

Rana catesbeiana showed a much more positive relationship with the first axis than did any other species, indicating that its abundance relative to the rest of the community was higher as road density increased and the

spatial extent of herbaceous vegetation decreased. Additional patterns in community structure became apparent when species were assigned to guilds based on their breeding ecology and landscape complementation
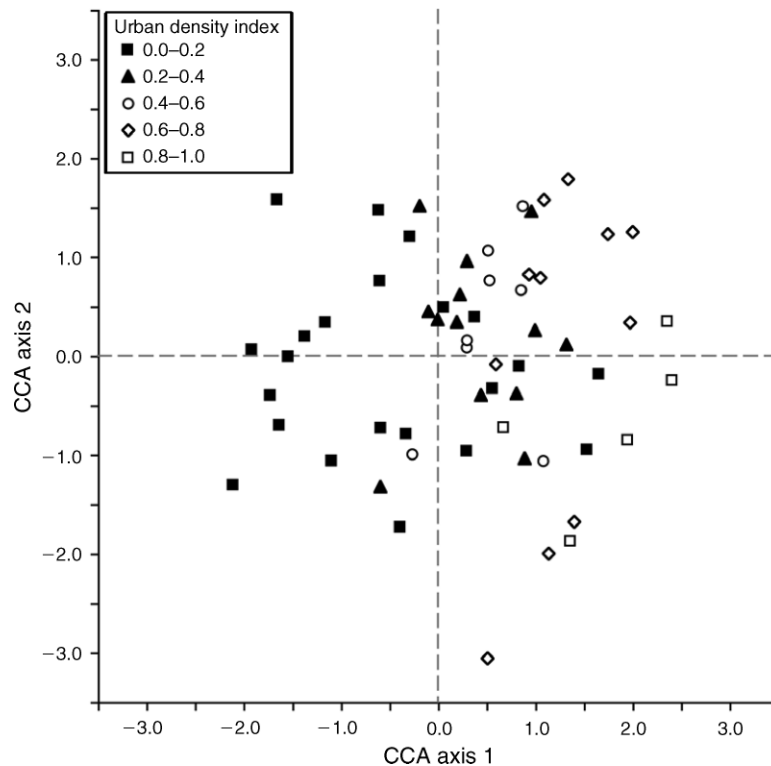
FIG. 4.   Location of sites in the space defined by the first two axes derived in canonical correspondence analysis (CCA), showing the relationship between the environmental gradients calculated in CCA and the index of urban density. Based on their urban density index scores, sites were divided into five quantiles (0 = least urban, 1 = most urban).

requirements (Table 1). The two species with positive axis 1 scores, *A. crepitans* and *R. catesbeiana*, occupy the same guild in three of the four types of guild classification: late breeding period, a preference for permanent ponds, and virtually no upland habitat use outside of the breeding season (Fig. 4).

DISCUSSION

Factors underlying anuran community structure

Our results indicated the pronounced effect of urban density on anuran abundance and diversity, consistent with the findings of others (e.g., Lehtinen et al. 1999, Ficetola and De Bernardi 2004, Riley et al. 2005, Rubbo and Kiesecker 2005). Urbanization also had a strong influence on anuran community structure. Landscape-scale factors in particular appeared to drive differential species abundance along the urban–rural gradient in central Iowa.

Overall, anuran community structure seemed to be most strongly influenced by the extent and contiguity of upland habitats, as well as the density and placement of roads in the surrounding landscape. These factors are undoubtedly linked, because an increase in road density reduces the amount and connectedness of herbaceous upland habitats. Our results indicate that species are differentially affected by the urban fragmentation of

upland habitats and dispersal routes, but that all species exhibit a negative association with urbanization (Fig. 3).

Based on our results, we predict that wetlands embedded in a matrix of unfragmented herbaceous vegetation with few roads will best accommodate *H. chrysoscelis* and *R. pipiens*, and to a lesser extent *B. americanus* and *P. triseriata*. *Rana catesbeiana* seems to be more resilient to urban fragmentation than most of the anuran community, though this may potentially be true to a lesser degree for *A. crepitans*. We would also expect that the abundance of *H. versicolor* relative to other anuran species will likely increase in areas with well-established, clustered wetlands surrounded by woody vegetation.

Examining the relative locations of different anuran guilds within the ordination space created by the first two CCA axes offers additional insights into the ecological processes underlying the observed patterns of community structure along the urban–rural gradient. *Bufo americanus*, *R. pipiens*, *H. chrysoscelis*, and *H. versicolor* all breed in mid to late spring, prefer temporary wetlands, and make extensive use of upland habitats outside of the breeding season. These species exhibited the strongest negative response to urban fragmentation in this study. By contrast, *R. catesbeiana* and *A. crepitans* both breed in late spring and summer and prefer wetlands with long hydroperiods, which may
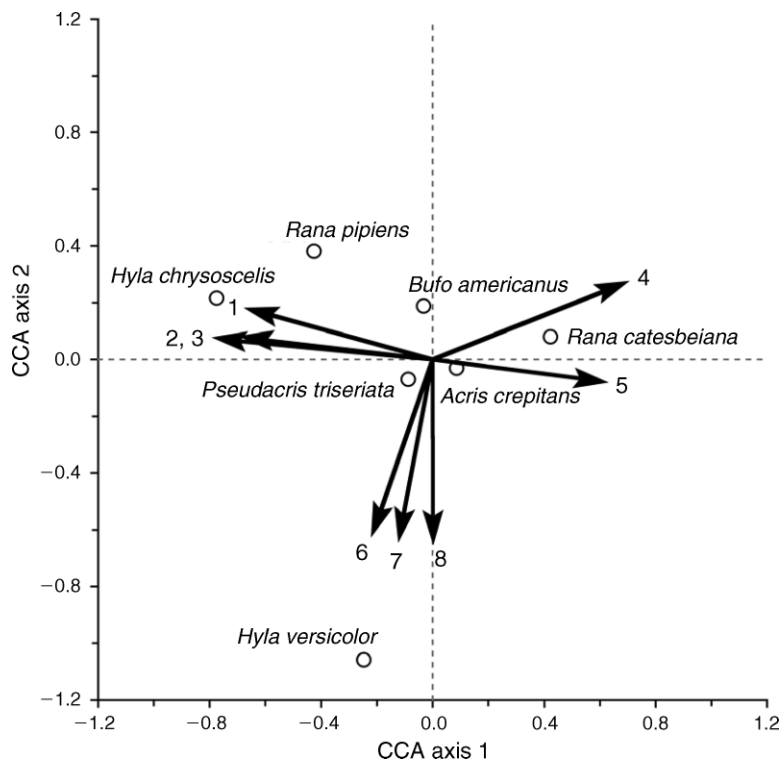
Fig. 5. Location of species relative to the first two axes derived in canonical correspondence analysis. Environmental variables (numbered) are represented by vectors; vector length indicates the relative weight of a given variable in the ordination, and direction indicates the correlation of that variable with each axis. Environmental variable means lie at the origin; above-average values of a given variable lie along its corresponding vector, and below-average values project from the origin in the direction opposite the arrow. The variables shown are (1) percent cover of herbaceous vegetation within 5 m, (2) mean area (ha) of herbaceous patches within 1 km, (3) percent cover of herbaceous vegetation within 1 km, (4) number of road crossings to the nearest other wetland, (5) percent cover of roads within 1 km, (6), wetland age (see Fig. 2 legend for a description of age categories), (7) percent cover of woody vegetation within 5 m, and (8) the patch density of surrounding wetlands within 1 km.

offer an additional explanation for their success relative to the rest of the anuran community. Because urban density is correlated with an increase in hydroperiod (Rubbo and Kiesecker 2005), they may have a competitive advantage over other species that are adapted to more ephemeral wetlands. Predation by *R. catesbeiana* suppresses the populations of other anurans (Kiesecker and Blaustein 1997, Pearl et al. 2004), potentially exacerbating the effect of urbanization on other native species by adding increased predation to the existing suite of factors negatively influencing anuran population persistence. It should be noted, however, that *A. crepitans* shows a much weaker association with urban fragmentation than does *R. catesbeiana*. It is located closer to *B. americanus* and *P. triseriata* in the ordination space created by the first two axes in CCA. Nonetheless, it is noteworthy that *A. crepitans* is fairly widespread in central Iowa's highly fragmented landscape. While *R. catesbeiana* has a long history as a human commensal species, *A. crepitans* is experiencing severe declines in the northern part of its range and has also declined in Iowa (Hay 1998, Lannoo 1998).

Considerations for amphibian conservation

The results of this study demonstrate the role of landscape connectivity and fragmentation in structuring anuran communities in urban areas. Amphibian conservation in urban landscapes requires a broad approach that promotes the functional connectivity of the greater landscape in addition to the protection and restoration of breeding sites. The composition and configuration of the matrix is vital for sustaining and enhancing a diverse anuran community. The importance of upland habitats and road density in structuring anuran communities, as indicated by this study, underscores that the protection, enhancement, and restoration of upland habitats between breeding sites is a key component maximizing the efficacy of conservation efforts.

Upland habitats have a direct and vital influence on the persistence of many anuran species, because they allow adults to survive winter migrations and juveniles to survive dispersal from their natal wetlands. Although juveniles of many species may disperse several kilometers or more to new breeding sites (Smith and Green 2005), little is known about the dispersal behavior and upland habitat use of many anurans (Rothermel 2004,

Stevens et al. 2004), especially in human-dominated landscapes. Because roads and other features of urbanized landscapes are barriers to dispersal (Fahrig et al. 1995, Vos and Chardon 1998, Forman and Deblinger 2000), there is likely high mortality with long dispersal distances.

Additionally, there is increasing evidence that landscape composition and configuration influence anuran populations at spatial scales much larger than those typically employed in landscape ecology studies. Houlahan and Findlay (2003) found a significant influence of land use at scales of 2–3 km, and Gibbs et al. (2005) found strong spatial autocorrelation in species occurrences at up to 10 km. There may be, therefore, broad-scale constraints on the use of available habitat across the landscape that are unaccounted for in most landscape ecology studies. The further study of the ecological mechanisms underlying these patterns would greatly increase our understanding of broad-scale population regulation and our ability to successfully promote long-term population persistence in urban landscapes.

Overall, our results illustrate that the habitat fragmentation and loss accompanying urbanization can be a driving force behind anuran community structure. Urbanization is a powerful agent of ecological change on the landscape, and has proven detrimental to many different taxa (McKinney 2002); we have illustrated that this phenomenon has a cascade of effects influencing the anuran community at spatial scales ranging from individual wetlands to broad landscapes. The next step in amphibian conservation biology, however, is to transcend this broad generalization and work to develop effective strategies for maintaining amphibian diversity in urban landscapes. Better integrating natural processes into the places where people live and work not only helps sustain biological diversity in an increasingly degraded world, but gives nature a needed immediacy to the public, helping to reinforce a broad conservation ethic while increasing quality of life (Miller and Hobbs 2002, Boyer and Polasky 2004, Turner et al. 2004, Miller 2005). Focusing efforts on urban nature conservation will also create more attractive, livable urban communities, potentially reducing development pressures in peri-urban areas (Merrill 2004, Santelmann and Larson 2004). The long-term success of amphibian conservation, however, relies on a sustained effort toward understanding the specific mechanisms driving community structure and species distributions in the built environment, and in using that mechanistic understanding to most effectively conserve and restore amphibian populations.

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APPENDIX A

Descriptions and locations of 61 central Iowa, USA, wetlands surveyed March–July 2005 (*Ecological Archives* A018-038-A1).

APPENDIX B

Data collection procedure for all variables of anuran breeding habitat and landscape structure for 61 central Iowa, USA, wetlands surveyed, March–July 2005 (*Ecological Archives* A018-038-A2).