Effects of Landscape Composition and Wetland Fragmentation on Frog and Toad Abundance and Species Richness in Iowa and Wisconsin, U.S.A.

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Abstract: *Management of amphibian populations to reverse recent declines will require defining high-quality habitat for individual species or groups of species, followed by efforts to retain or restore these habitats on the landscape. We examined landscape-level habitat relationships for frogs and toads by measuring associations between relative abundance and species richness based on survey data derived from anuran calls and features of land-cover maps for Iowa and Wisconsin. The most consistent result across all anuran guilds was a negative association with the presence of urban land. Upland and wetland forests and emergent wetlands tended to be positively associated with anurans. Landscape metrics that represent edges and patch diversity also had generally positive associations, indicating that anurans benefit from a complex of habitats that include wetlands. In Iowa the most significant associations with relative abundance were the length of the edge between wetland and forest (positive) and the presence of urban land (negative). In Wisconsin the two most significant associations with relative abundance were forest area and agricultural area (both positive). Anurans had positive associations with agriculture in Wisconsin but not in Iowa. Remnant forest patches in agricultural landscapes may be providing refuges for some anuran species. Differences in anuran associations with deep water and permanent wetlands between the two states suggest opportunities for management action. Large-scale maps can contribute to predictive models of amphibian habitat use, but water quality and vegetation information collected from individual wetlands will likely be needed to strengthen those predictions. Landscape habitat analyses provide a framework for future experimental and intensive research on specific factors affecting the health of anurans.*

Efectos de la Composición del Paisaje y la Fragmentación de Humedales en la Abundancia de Ranas y la Riqueza de Especies en Iowa y Wisconsin, U.S.A.

Resumen: *El manejo de poblaciones de anfibios para revertir disminuciones recientes requerirá de la definición de hábitats de alta calidad para ciertas especies o grupos de especies, seguido de esfuerzos para retener o restaurar estos hábitats o paisajes. Examinamos relaciones de hábitat a nivel de paisaje para sapos y ranas midiendo asociaciones entre la abundancia relativa y la riqueza de especies en base a datos de muestreos derivados de llamadas de anuros y características de mapas de cobertura del suelo para Iowa y Wiscon-*

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sin. Los resultados mas consistentes fueron para todas las asociaciones de anuros teniendo una relación negativa con la presencia de tierras urbanas. Los bosques altos y de humedales y los humedales emergentes tendieron a estar positivamente asociados con los anuros. Las mediciones de paisaje que representan bordes y diversidad de parches también mostró asociaciones positivas, indicando que los anuros se benfician de una complejidad de hábitats que incluyen a los humedales. En Iowa, las asociaciones mas significativas con la abundancia relative fueron la densidad del bosque de humedal (positiva) y la presencia de tierras urbanas (negativa). En Wisconsin, las dos asociaciones mas significativas con la abundancia relativa fueron el área forestal y el área agricultural (ambas positivas) Los anuros tuvieron asociaciones positivas con la agricultura en Wisconsin, pero no en Iowa. Los parches remanentes de bosque en paisajes agriculturales puedon estar aportando refugio para algunas de las especies de anuros. Las diferencias en asociaciones de anuros con la profundidad del agua y humedales permanentes entre los dos estados sugiere oportunidades para acciones de manejo. Mapas de gran escala pueden contribuir en modelos de predicción de uso del hábitat por anfibios, pero la información colectada sobre calidad del agua y vegetación en humedales individuales será probablemente necesaria para fortalecer estas predicciones. El análisis de paisaje provee un marco para la investigación experimental e intensiva a futuro sobre los factores específicos que afectan la salud de los anuros.

Introduction

In much of the world, including North America, amphibian populations are in decline (Blaustein & Olson 1991; Lannoo 1998; but see also Pechmann & Wilbur 1994). The causes of these declines are under investigation, but emerging evidence indicates that landscape-scale factors may be contributing to declines in some locations. Management of amphibian populations to reverse declines will require defining high-quality habitat for individual species or groups of species, followed by efforts to retain or restore these habitats on the landscape. Wetland maps, developed by state and federal agencies to document and protect wetland habitats (Wilen & Bates 1995), can be used to identify potential amphibian breeding habitats and to focus restoration efforts.

Variables measured at the landscape level, such as the density of roads or the area of forests and wetlands surrounding breeding ponds, have been shown to be correlated with amphibian presence or absence and species richness (Beebee 1985; Findlay & Houlahan 1997; Dodd & Cade 1998; Vos & Chardon 1998). Forests and other natural habitats can serve as corridors for amphibian movement, whereas roads and other hostile environments may be barriers to movement (Gibbs 1998). Therefore, both the presence and arrangement of landscape features such as forests and roads can influence population levels. Amphibian populations may be depressed in agricultural landscapes because of vulnerability to environmental contaminants (Berrill et al. 1997; Howe et al. 1998). Agricultural chemicals may also be reducing the quality of wetland breeding habitats adjacent to tilled fields (Hanson et al. 1994; Freemark & Boutin 1995). Distance to the next nearest pond has been shown to influence populations and species richness and is likely linked to amphibian dispersal ability (Vos & Stumpel 1995; Halley et al. 1996). If specific habitat relationships such as these can be identified, it is possible to project how future land-use change will affect amphibian populations (Cole et al. 1997; White et al. 1997).

We examined landscape-level habitat relationships for frogs and toads (anurans) by measuring associations between relative abundance and species richness based on survey data derived from anuran calls and features of land-cover maps for Iowa and Wisconsin (U.S.A.), two midwestern states with high agricultural land use. We developed a priori hypotheses for relationships we expected to find, based on habitat preferences described in the literature. We expected that anurans preferring to breed in temporary wetlands would be associated with temporary wetlands and that anurans preferring permanent water would be associated with deep-water habitats. Because anurans breed near wetland edges, we expected that most anurans would be associated with landscape metrics representing high patch diversity and wetland edge length. We expected that anurans requiring forest or shrub habitats during part of the year would be associated with forests. Because of the intensity of human disturbance, we expected that most anurans would be negatively associated with agricultural and urban areas.

Methods

Survey Methods

We used surveys of anuran calls conducted by volunteers in the states of Iowa (Hemesath 1998) and Wisconsin (Mossman et al. 1998) as a measure of the relative abundance and richness of species at each survey point. Wisconsin and Iowa have been leaders in the development of annual statewide anuran calling surveys; few states have collected such extensive data over multiple years. Volunteer surveys are the only source of information on amphibian populations over regions as large as states and are critical components of state-level amphibian monitoring programs (Shirose et al. 1997). Roadside survey locations were selected subjectively by volunteer observers. Volunteers were provided with training tapes and specific protocols regarding data collection and recording. All surveys were conducted at night. Anurans (see Table 1 for list of species) were surveyed three times each breeding season at each survey point, with the timing analogous between the states but adjusted to accommodate differences in latitude. In Iowa those times were 1-28 April, 7 May-4 June, and 13 June-10 July. In Wisconsin they were 8-28 April, 20 May-5 June, and 1-15 July. The relative abundance of each species was recorded as a call index value of 1, 2, or 3 (few, some, and many, respectively).

We identified a peak breeding time period for each species based on its maximum calling periods. Data were included for a species at a particular point if the survey was conducted during a peak breeding time period at least three times from 1991 to 1995. The maximum call index value at a survey point was defined as the abundance index of the species at that point. The maximum value represents the highest population level an individual survey location could produce for a given species—the wetland at its best. We included in the analysis all survey points that met the above criteria, that were within the range for each species (Christiansen & Bailey 1991; Casper 1996; Mossman et al. 1998), and that were ≥2000 m apart. Survey locations were well distributed across both states (n = 118 in Iowa; n = 260 in Wisconsin).

Guild Classification and Landscape Variables

Anuran species were grouped into guilds to examine how species with similar life-history characteristics were related to landscape features. The guilds were based on preferred habitat during the breeding, nonbreeding, and hibernation seasons (Table 1). Classifications were derived from published literature for the upper Midwest (Vogt 1981; Christiansen & Bailey 1991; Oldfield & Moriarty 1994) and from expert opinion (R. Hay, personal communication).

The anuran survey points were located on and digitized from U.S. Geological Survey 7.5-minute quadrangle maps. A buffer of 1000 m radius around each survey point was determined to be the smallest that the scale limitations of the spatial data would allow. This distance was found to be optimal in a similar analysis of treefrog habitat associations in Europe (Vos & Stumpel 1995). The area measured was much larger than the home range for most anurans but smaller than the maximum dispersal distance recorded for some anurans (Stebbins & Cohen 1995); it therefore represents a reasonable area of landscape influence from a metapopulation perspective.

Several geographical information system data sets were used to obtain the landscape variables used in the analysis. Digitized maps (scale = 1:24,000) of the locations and attributes of wetlands in Iowa were obtained from the U.S. Fish and Wildlife Service (1981-1992) Na-

Table 1. Anuran species names, preferred breeding period, and guild associations for study sites in Iowa and Wisconsin.*

			Breeding[b]		*Nonbreeding*[c]			*Hibernation*[d]		
Scientific name	*Common name*	*breeding period*[a]	*perm. water*	*temp. water*	*water*	*forest/ litter*	*open*	*water*	*forest/ litter*	*ground*
Rana sylvatica	wood frog	1	0	1	0	1	0	0	1	0
Pseudacris triseriata	chorus frog	1	0	1	0	1	1	0	1	0
Pseudacris crucifer	spring peeper	1	0	1	0	1	0	0	1	0
Rana pipiens	leopard frog	1	1	1	1	0	1	1	0	0
Rana palustris	pickerel frog	1	1	0	1	1	1	1	0	0
Bufo americanus	American toad	2	1	1	0	1	1	0	1	0
Hyla versicolor	eastern gray treefrog	2	1	1	0	1	0	0	1	0
Hyla chrysoscelis	Cope's gray treefrog	2	1	1	0	1	1	0	1	0
Acris crepitans	cricket frog	3	1	0	1	0	0	0	1	0
Rana septentrionalis	mink frog	3	1	0	1	0	0	1	0	0
Rana clamitans	green frog	3	1	0	1	0	0	1	0	0
Rana catesbeiana	bullfrog	3	1	0	1	0	0	1	0	0
Bufo cognatus	Great Plains toad	2	1	1	0	0	1	0	0	1
Bufo woodhousii	Woodhouse/Fowler's toad	2	0	1	0	0	1	0	0	1

**Species that can successfully survive or reproduce in a habitat during the identified life-history phase are identified with a 1; those that do not with a 0.*

[a] *1, April; 2, May; 3, June-July.*

[b] *Will breed in permanent water or temporary (ephemeral) ponds.*

[c] *Active, nonbreeding portion of the year is spent in the water or along the water edges, in trees or forest litter, or in open, nonforested habitats (grasslands).*

[d] *Hibernation or estivation period is spent in or near water, in forest litter, or underground.*

tional Wetland Inventory (NWI) (http://www.nwi.fws.gov) (Cowardin et al. 1979; Wilen & Bates 1995). Maps for Wisconsin were obtained from the Wisconsin Wetland Inventory (WWI) (Wisconsin Department of Natural Resources 1984–1996; scale = 1:24,000) and the Wisconsin hydrology coverages (U.S. Geological Survey 1987–1996; scale = 1:100,000). U.S. Geological Survey (1986) land use and land cover (LULC) maps (scale = 1:250,000) were used for both states. We created maps that included general information about land-cover types and detailed information about wetland areas by overlaying the NWI/WWI polygon coverages on the LULC coverages. The maps were generalized into the following classes: forest, agriculture, urban, open water, emergent wetland, and forested wetland (Table 2).

We used the FRAGSTATS Spatial Pattern Analysis (McGarigal & Marks 1994) software to calculate several landscape metrics for each buffer area (Table 2). The NWI/WWI data sets included line (Iowa only) and point coverages of wetlands too small to be mapped as polygons. We included as additional variables the sum of the length of these lines and the total counts of these wetlands for each buffer. The landscape variables used in the analysis were grouped into composition, diversity-edge, and patch variables (Table 2).

Statistical Methods

We analyzed the data for each state separately because of differences in latitude and because management applications of the research will be implemented at the state level. We conducted multiple regression analyses to examine how individual landscape variables were associated with anuran abundance and richness. The distributions of the landscape variables were screened for fit with model assumptions, and the urban variable

Table 2. Pearson correlation coefficients (expressed as percentages) between landscape variables and principal component factors for Iowa (IA) and Wisconsin (WI).

	Principal component factors[a]									
	FORESTED WETLAND		*UPLAND FOREST*		*EMERGENT WETLAND*		*LAKE*		*URBAN*	
Landscape attribute	*IA*	*WI*	*IA*	*WI*	*IA*	*WI*	*IA*	*WI*	*IA*	*WI*
Composition										
Forest area (FOR)	1	−16	82[b]	80[b]	−38	−38	−4	12	−12	−19
Agricultural land area (AGR)	−34	−25	−77[b]	−70[b]	8	19	−40	−52	−11	4
Presence/absence of urban land (URB)	4	0	4	−12	−2	3	0	15	95[b]	91[b]
Area of water in buffer (WATER)	4	−7	15	5	10	−5	92[b]	84[b]	0	17
Area of emergent wetlands (wetlands with emergent vegetation) (EMERG)	0	5	6	−6	84[b]	83[b]	15	17	−8	−12
Area of forested wetlands (WFOR)	95[b]	94[b]	16	12	5	−1	−3	13	−1	−3
Area of temporary wetlands (TEMPW)	91[b]	93[b]	20	4	27	13	−4	−9	−3	−6
Area of permanent wetlands (PERMW)	1	8	13	10	29	23	92[b]	88[b]	−3	5
Length of linear wetlands (Iowa only) (WET_M)	15	—	32	—	14	—	−43[b]	—	−28	—
Small wetlands mapped as points (WET_CT)	−16	−3	41	44	47[b]	−11	−25	−12	1	59[b]
Diversity/edge										
Edge density (m of edge/ha) of emergent wetlands (EMERGED)	16	6	0	−9	87[b]	92[b]	18	7	−6	−1
Edge density (m of edge/ha) of forested wetlands (WFORED)	85[b]	71[b]	32	55	16	8	6	2	7	22
Length of edge between forest and all wetlands, including water (EDGFO)	31	26	72[b]	81[b]	−7	−15	−6	17	0	8
Length of edge between agriculture and all wetlands, including water (EDGAG)	28	13	−3	−34	78[b]	62[b]	16	−41	7	10
Length of edge between urban land and all wetlands, including water (EDGUR)	1	5	9	−2	−1	7	4	16	94[b]	91[b]
Shannon diversity of patch types/areas (SHDI)	46	42	69[b]	10	21	47[b]	28	46	27	18
Patch										
Fractal dimension (area-weighted mean) of emergent wetlands (EMERGF)	13	−1	−23	−6	43[b]	75[b]	−7	1	1	6
Fractal dimension (area-weighted mean) of forested wetlands (WFORF)	27	29	53[b]	53[b]	23	30	10	−14	18	7
Percent variance explained by factor	28.9	13.5	16.2	21.4	12.3	24.2	10.2	10.9	7.2	6.9
Total variance explained by the 5 factors: IA = 74.9%, WI = 76.8%										

[a] *Principal component factors were named based on the strength of these coefficients.*
[b] *Strongest correlation for each variable within a state.*

(URB) was found to have a skewed distribution; it was converted from area to presence-absence. Regression analyses using individual landscape variables can be directly applied to future predictive models; they explained a higher proportion of variation than the principal components (PC) variables (below) and provided the most information about landscape features such as edge density and patch diversity. The PC analyses were used to simplify the landscape data, eliminate problems with intercorrelation of individual variables, reduce the number of variables, and provide a composite picture of anuran habitat associations. The two methods together provide complementary information on anuran habitat associations.

In the PC analysis, we used the principal axis method to extract the components and followed this with a varimax (orthogonal) rotation (SAS Institute 1990). We used multiple regression to assess the relationship between landscape variables and the sum of abundance values for all species combined and species grouped by guild associations. Mallow's C_p statistic was used to find the most parsimonious subset of significant variables. We used the PC factors to run a second regression. The proportion of species out of all possible species occurring at a point was used as a measure of species richness. The relationship between the arcsin square root-transformed proportion and the landscape variables was examined with multiple regression on the individual variables and, in a second analysis, with the PCs. We tested our a priori hypotheses by looking for significant associations between anuran abundance and species richness and specific landscape variables.

Results

In the PC analysis of the individual landscape variables, the first five PC factors had eigenvalues of >1 in both Iowa and Wisconsin and were retained for rotation. Factors 1-5 accounted for 75% (Iowa) and 77% (Wisconsin) of the total variance. In both states, the individual variables related to the PC factors similarly, so the factors were labeled with a name common to both states (Table 2).

Our individual variable models generally explained more variation than the PC factor models. When anuran abundance indices were the dependent variables, the individual variable regression models accounted for 8-20% of the variance in the data sets. When PC factors were used, the regression models accounted for 2-17% of the variance. The habitat associations for relative abundance and species richness were generally similar within a state (Table 3). When species richness was the dependent variable, the individual variable regression models accounted for 2-19% of the variance in the data sets. When PC factors were used with species richness, the regression models accounted for 1-15% of the variance.

The most consistent result across all anuran guilds was a negative association with the presence of urban land (URB, URBAN; Table 3). Upland and wetland forests (FOR, WFOR) and emergent wetlands (PERMW, EMERGENT WETLAND) tended to be positively associated with anurans. Landscape metrics that represent edges and patch diversity (WFORED, SHDI) also had generally positive associations, but the results were less consistent across all guilds. In Iowa the most significant associations with relative abundance were the length of the wetland-forest edge (positive) and the presence of urban land (negative) (Fig. 1). In Wisconsin the two most significant associations with relative abundance were forest area and agricultural area (both positive; Fig. 2).

Discussion

The PC analysis of the landscape variables was remarkably similar between the two states. The PC factors correlated with similar suites of variables, indicating that similar land-cover types tend to occur together on the landscape. The states differed with respect to which PC factors explained the most variation in the landscape data. In Iowa, where forests are relatively rare, forested wetlands (FORESTED WETLAND) accounted for the most variation (Table 2). In Wisconsin, where forests are more common, emergent wetlands (EMERGENT WETLAND) accounted for the most variation.

Permanent and Ephemeral Wetlands

We expected that anurans preferring to breed in temporary wetlands would be associated with temporary wetlands and that anurans preferring permanent water would be associated with deep-water habitats. Contrary to our expectations, temporary wetland area (TEMPW), the length of small streams (WET_M), and the number of small wetlands (WET_CT), all variables associated with temporary wetlands, contributed little to our models. In Wisconsin, many anurans were associated with permanent-water variables (PERMW and LAKE; Table 3). Conversely, some Iowa anurans were negatively associated with deep-water variables (WATER, LAKE).

Temporary and permanent water anuran guilds may not relate closely to our wetland classifications partly because wetland characteristics can change from year to year because of climatic conditions. Our results suggest differences in the quality of deep-water habitats and permanent wetlands between the two states. Wisconsin has many more natural lakes than Iowa because of its glacial history. In Iowa, most large water bodies are reservoirs, created by damming rivers and streams for water control or recreational purposes. Natural lakes commonly have extensive, shallow wetland complexes associated with them, whereas reservoirs do not. Wetland complexes

Table 3. Significant associations between habitat variables and maximum abundance index (A) and species richness (S) for all species and guilds in Iowa (I) and Wisconsin (W).[a]

Habitat variables[b]	All species				Breeding								Nonbreeding												Hibernation											
					permanent water				temporary water				water				forest/litter				open				water				forest/litter				ground			
	A		S		A		S		A		S		A		S		A		S		A		S		A		S		A		S		A		S	
	I	W	I	W	I	W	I	W	I	W	I	W	I	W	I	W	I	W	I	W	I	W	I	W	I	W	I	W	I	W	I	W	I	W	I	W
Individual																																				
FOR		P		P		P		P		P		P		P		P		$P^{*,+}$		$P^{*,+}$	N	P				P		P		$P^{*,+}$		$P^{*,+}$		—		—
AGR		P^{*}		P^{*}		P		P		P	N	P		P		P	N	P	N	P		P^{*}		P^{*}		P	N	P		P		P	P^{*}	—	P^{*}	—
URB	$N^{*,+}$	$N^{*,+}$	$N^{*,+}$	$N^{*,+}$	N	N	N	N	N	N		N	N	N	N		N	N		N					N		N		N	N		N		—		—
WATER	N				N^{*}							N	N^{*}			$P^{*,+}$				N								$P^{*,+}$						—		—
WFOR		P		P		P		P		P						P		$P^{*,+}$		$P^{*,+}$								P		$P^{*,+}$				—		—
PERMW		P		P		$P^{*,+}$		$P^{*,+}$		P		P		$P^{*,+}$		$P^{*,+}$		P		P		P	P	P		$P^{*,+}$				P		P		—		—
WFORED	$P^{*,+}$		$P^{*,+}$		P	N			P		P	P	P		P	N												N				$P^{*,+}$		—	P^{+}	—
EDGFO																													$P^{*,+}$		$P^{*,+}$			—	P	—
SHDI		$P^{*,+}$		$P^{*,+}$		P		P		P	N			P	N	P		P		P						P	N	P		P				—		—
Principal component factor																																				
FORESTED WETLAND	P		P		P				P		P		P				$P^{*,+}$				P	N			P									—	P	—
UPLAND FOREST	P	P		P	P					P	P	P	P				$P^{*,+}$	$P^{*,+}$	$P^{*,\dagger}$	$P^{*,+}$	N	N		N				N	$P^{*,+}$	$P^{*,+}$	$P^{*,+}$	$P^{*,+}$	N	—		—
EMERGENT WETLAND		$P^{*,+}$		$P^{*,+}$	P	P		P		P		P	P	P	P	P		P			P	P		P	P	P	P	P						—		—
LAKE		P		P	N^{*}	$P^{*,+}$		$P^{*,+}$		P		P	N^{*}	$P^{*,+}$		$P^{*,+}$							P	P		$P^{*,+}$		$P^{*,+}$		P				—		—
URBAN	$N^{*,+}$	$N^{*,+}$	$N^{*,+}$	$N^{*,+}$	N	N	N	N	N	N		N	N	N	N	N	N	N		N		N		N	N	N	N	N	N	N		N		—		—

[a]Habitat variables that contributed to a significant model are shown as P (positive) or N (negative) in their association with the guild response variables. Relationships subject to a priori hypotheses are marked with an asterisk (*); relationships in the expected direction are marked with a plus sign (+). Other associations emerging from the regression models are shown, but were not included in a priori hypothesis.
[b]Abbreviations defined in Table 2.

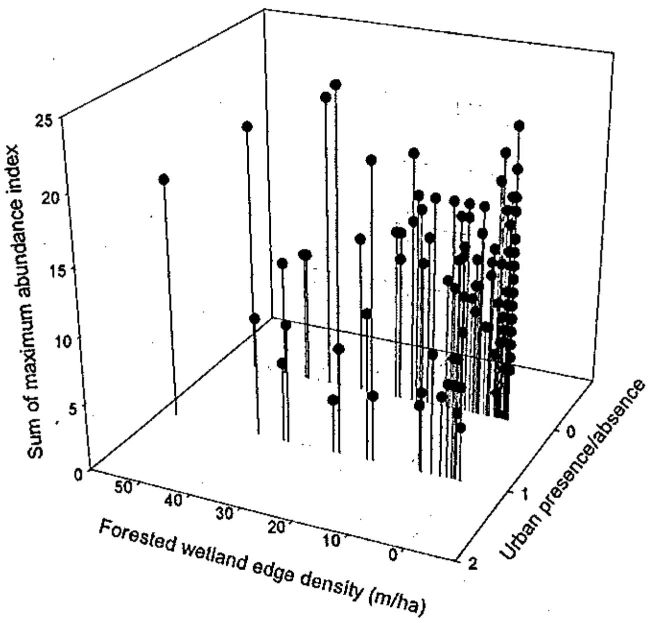

Figure 1. Iowa data for forested wetland edge density, urban presence or absence, and the sum of maximum abundance indices for all species.

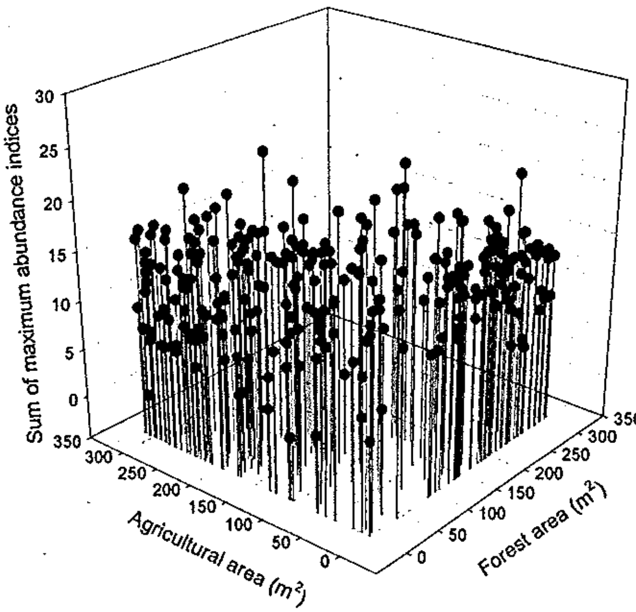

Figure 2. Wisconsin data for forest area, agricultural area, and the sum of maximum abundance indices for all species.

adjacent to lakes likely enhance habitat quality for anurans by providing productive, shallow-water areas with less predation pressure during breeding. There is potential for creating productive amphibian habitat in association with reservoirs if design features critical for amphibians are identified. Our results may also reflect differences in management of permanent wetlands between the two states. Because fish (Hecnar 1997; Laurila & Aho 1997) and bullfrogs (Kiesecker & Blaustein 1997; Kupferberg 1997) are predators on and competitors with amphibian larvae (e.g., Lannoo 1996), differences in wetland fish or bullfrog stocking practices between the states could have different effects on amphibian populations.

Diversity and Edges

We expected that most anurans would be associated with landscape metrics representing high patch diversity and wetland edge length. This was generally true: anurans were more abundant and diverse where habitat patch diversity (SHDI) was high (Wisconsin) or where there were forested wetland edges (WFORED; Iowa) (Table 3). Anurans appeared to benefit from a complex of habitats, especially wetland habitats and forests adjacent to wetlands. Mann et al. (1991) found that the probability of anuran species occurrence increases as the number of pools increases, a result consistent with our findings. Marsh and Pearman (1997) found evidence that some species of forest-dwelling frogs in Ecuador are sensitive to forest fragmentation. If anurans in Iowa and Wisconsin are negatively affected by habitat fragmentation, we would expect to find negative associations with landscape variables measuring edge, fractal dimension, and patch diversity. We did not find such evidence, but the small distance surrounding each survey point limited our ability to infer fragmentation effects at larger geographic scales.

Forests

We expected that anurans requiring forest or shrub habitats during part of the year would be associated with forests. We found consistent, positive associations between anurans and both upland (FOR, UPLAND FOREST) and wetland forests (WFOR, FORESTED WETLAND) in both states (Table 3). Forest variables had positive associations for many anuran guilds, not just those that require forests during some part of their life cycle. We found anurans associated with forests where forests are common (Wisconsin) and where forests are relatively scarce (Iowa).

Why are forests important habitats for anurans when wetlands are their primary breeding habitats? Forests provide necessary habitat for many species that spend part or all of their nonbreeding season in trees, shrubs, or heavy litter. Forests may also be associated with anurans because they represent relatively undisturbed habitat compared with agricultural or urban areas. The structure of trees, shrubs, and forbs in a forest creates diverse habitats with many niches. Besides providing structural niches, forests moderate the temperature and evaporation rate of aquatic habitats adjacent to them, contribute organic matter, and add diversity to the plant and animal community in the area (Waldick 1997). These factors, in turn, affect other community relationships such as trophic and predator-prey interactions. Forests may also provide dispersal corridors for anuran movement between breeding and nonbreeding habitats (Laan & Verboom 1990; Waldick 1997). Remnant forest patches in agricultural landscapes, although small and isolated, may provide refuges for some anuran species. Tilled fields are probably inhospitable for many species (Bonin et al. 1997).

The association between forests and amphibians is one of the most consistent landscape-scale habitat relationships reported in the literature. Findlay and Houlihan (1997) found that higher herptile species richness is associated with high forest cover within 2 km of a wetland. Bonin et al. (1997) found several anuran species associated with forest in Quebec; fragmentation of those forests did not affect their occurrence. Hecnar (1997) also found a strong association between amphibian species richness and the percentage of woodland within 2 km of the breeding pond in Ontario. Laan and Verboom (1990) found that amphibian species richness is positively influenced by woodland near the breeding pond, and Strijbosch (1980) found that amphibians prefer deciduous to coniferous forests. Mitchell et al. (1997) found that amphibians require a combination of forest and wetland habitats in Virginia.

Agriculture

We expected that most anurans would be negatively associated with agriculture. We failed to find strong negative associations between anurans and agriculture. Agricultural area (AGR) was positively associated with anurans in Wisconsin but not in Iowa (Table 3). Other studies have identified negative associations with agriculture. Hecnar (1997) found decreases in amphibian diversity associated with intensive agricultural landscapes in Ontario. Bonin et al. (1997) also found that anuran species richness is inversely related to agricultural monocultures.

Modern farming practices often lead to habitat loss: draining and filling of wetlands, conversion of natural habitats to intensively managed annual monocultures, soil compaction, and disturbance for anurans spending time underground (Bonin et al. 1997). In addition, the use of herbicides and pesticides presumably has negative effects on the physiology of anurans in or adjacent to crop fields. Runoff from agricultural lands can move these contaminants considerable distances from their point of application, into wetlands and streams. The positive associations with agriculture we found in Wisconsin may be due to the moderating effect of forests described above. Wisconsin's climate and geology favor forests and restrict intensive row-crop agriculture to smaller portions of the state. In Iowa, where more intensive agriculture is practiced, a few negative associations with agriculture were found among species that require temporary wetlands or forests during some part of the year. Some agricultural crops (hay) or practices (grazing) may be more favorable to anurans than others (annual row crops) because of lower disturbance or less use of agricultural chemicals. We used a general agricultural classification that combined grazed land and row crops. Distinguishing among different types of agriculture may help refine models, but crop rotation over short time intervals complicates this approach.

Despite the risks, midwestern anuran populations coexist with agriculture because it is the dominant land use in this region. We suggest that anuran populations in intensive row-crop agriculture are dependent upon adjacent, less disturbed environments, such as forests, grasslands, emergent wetlands, lakes, and streams. Even small areas of these other cover types may be important in maintaining anuran populations on the landscape. The close relationship between anurans and agriculture has many potential implications for management. For example, perhaps anurans should be included in the testing of new agricultural chemicals prior to government approval (Howe et al. 1998).

Urban

We expected that most anurans would be negatively associated with the presence of urban land. Negative associations with urban land use (URB, URBAN) were found across most anuran guilds in both states (Table 3). Urban areas are unfriendly habitat for anurans because of conversion of natural habitats to roads, home sites, and industrial uses and because of contamination of wetlands. Urban wetlands, often found in parks, experience high human use and are excavated and stocked with fish. Chemicals widely applied to lawns and golf courses may have a negative effect, given anuran vulnerability to toxins in water. Anurans migrating between breeding and nonbreeding areas experience high mortality at road crossings (Ashley & Robinson 1996), which could have serious effects on populations due to adult mortality prior to breeding. Findlay and Houlahan (1997) found that species richness of herptiles is negatively correlated with the density of paved roads within 2 km of the wetland. Vos and Chardon (1998) found a negative relationship between road density and the probability of occurrence of the moor frog (*Rana arvalis*). Delis et al. (1996) found that amphibian populations were lower at a developed urban site than at an undeveloped park nearby. In addition, they had concerns about urban encroachment degrading the park over time. Our results contrast with those of Hecnar (1997), who found a positive correlation between amphibian richness and human population density.

Urban sprawl is a pervasive phenomenon in the United States and results in permanent loss of natural habitats and fragmentation of those that remain (Matlack 1997). Models projecting land development can be used to predict effects on biodiversity for amphibians and other taxa (White et al. 1997). The potential effects of urban sprawl on amphibians could be serious, even in rural states like Iowa and Wisconsin. We need to investigate why urban areas have such a strong negative association with anuran relative abundance and richness, and we need to identify ways to improve habitat quality in areas of high human population density.

Management Implications

Anurans respond to environmental factors at several spatial scales. Both intensive field studies at a few sites and extensive multisite monitoring will be needed to identify most of the habitat variables important to anurans. Water quality and vegetation information collected from individual wetlands will be needed to refine predictive models. Munger et al. (1998) found associations between NWI classifications and two frog species in southwestern Idaho, but a combination of NWI classifications and on-site habitat variables performed better. Even though we were able to identify some important relationships between anuran populations and landscape variables, the explanatory power of our landscape habitat models may have been reduced by the subjective selection of study sites, which potentially underrepresents poor sites for anurans (i.e., locations without wetlands). In addition, land cover for some sites, especially those near urban areas, may have changed since the creation of the maps we used. Other researchers have also discovered that landscape variables alone explained <35% of the statistical variation in their data sets (Bonin et al. 1997; Hecnar 1997). In contrast, Beebee (1985) found that pond characteristics, including water chemistry, are not as predictive of amphibian diversity as are landscape variables. Hecnar and M'Closkey (1996) found that water chemistry explains 19% of the variance in amphibian species richness in their study. In a long-term study of amphibians and reptiles, Gibbons et al. (1997) conclude that spatially extensive, long-term monitoring, standardized for level of effort, was needed to accurately gauge biodiversity at their site.

Analyses of broad-scale habitat associations would be impossible without the availability of anuran survey data and wetland maps distributed across large areas, such as states. Knowledge of broad habitat associations is critical if we hope to reverse declines in amphibian populations. States should continue to develop monitoring programs that collect landscape-scale information on amphibian populations. Maps of land cover and wetlands should be designed for multiple uses, including the development of habitat models for species of concern. Issues of spatial resolution and accuracy, vegetation classifications, temporal accuracy in terms of land-use changes, and standardization across geopolitical boundaries are all important considerations that affect the success of habitat modeling.

The habitat relationships we identified provide managers with clues to restoring anuran habitats in areas where populations are low or declining. In general, wildlife managers can use landscape analyses, along with range maps and population trend analyses, to get a comprehensive picture of the health of anuran populations in a state or region. In addition, our work points out problems deserving more intensive research, such as the problems facing anurans living in urban environments and the variable quality of permanent wetlands. Landscape analyses can provide a framework for future experimental research on specific factors affecting the status of anuran populations.

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