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Landscape Associations of Frog and Toad Species in Iowa and Wisconsin, U.S.A.

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Landscape habitat associations of frogs and toads in Iowa and Wisconsin were tested to determine whether they support or refute previous general habitat classifications. We examined which Midwestern species shared similar habitats to see if these associations were consistent across large geographic areas (states). *Rana sylvatica* (wood frog), *Hyla versicolor* (eastern gray treefrog), *Pseudacris crucifer* (spring peeper), and *Acris crepitans* (cricket frog) were identified as forest species, *P. triseriata* (chorus frog), *H. chrysocelis* (Cope's gray treefrog), *R. pipiens* (leopard frog), and *Bufo americanus* (American toad) as grassland species, and *R. catesbeiana* (bullfrog), *R. clamitans* (green frog), *R. palustris* (pickerel frog), and *R. septentrionalis* (mink frog) as lake or stream species. The best candidates to serve as bioindicators of habitat quality were the forest species *R. sylvatica*, *H. versicolor*, and *P. crucifer*, the grassland species *R. pipiens* and *P. triseriata*, and a cold water wetland species, *R. palustris*. Declines of *P. crucifer*, *R. pipiens*, and *R. palustris* populations in one or both states may reflect changes in habitat quality. Habitat and community associations of some species differed between states, indicating that these relationships may change across the range of a species. *Acris crepitans* may have shifted its habitat affinities from open habitats, recorded historically, to the more forested habitat associations we recorded. We suggest contaminants deserve more investigation regarding the abrupt and widespread declines of this species. Interspersion of different habitat types was positively associated with several species. A larger number of wetland patches may increase breeding opportunities and increase the probability of at least one site being suitable. We noted consistently negative associations between anuran species and urban development. Given the current trend of urban growth and increasing density of the human population, declines of amphibian populations are likely to continue.

INDEX DESCRIPTORS: Landscape, Anuran, frog, toad, habitat, bioindicator.

Most of what is known about anuran habitat associations in the Upper Midwest is recorded in species accounts (Vogt 1981, Christiansen and Bailey 1991, Oldfield and Moriarty 1994). These accounts were derived primarily from the cumulative knowledge and experience of field biologists, rather than from quantitative data. Species accounts also tend to focus on habitat as defined by the type of breeding habitat (wetland) rather than the landscape context. Evidence is growing that surrounding landscapes may be as important to amphibians as the quality of the breeding site itself. The landscape influences dispersal, metapopulation dynamics, and inputs of nutrients and contaminants (Hecnar and M'Closkey 1996, 1998, Findlay and Houlahan 1997, Dodd and Cade 1998, Lehtinen et al. 1999). In Wisconsin, several species with declining population trends spend large portions of their lives in upland habitats, so an assessment of these habitats is warranted (Mossman et al. 1998). Traditional species accounts also tend to assume that habitat associations are consistent across the ranges of species.

Anurans have been proposed as indicators of wetland habitat quality because of their widespread occupancy of wetlands and their vulnerability to environmental hazards at the breeding site (Vitt et al. 1990). Species useful as bioindicators are common enough to be

routinely identified in specific habitats, but disappear from the most degraded sites (Angermeier and Karr 1994). Amphibians have permeable skin (Jorgensen 1997), a complex life history, and adult, egg, and larval stages are exposed to toxic herbicides and pesticides at aquatic breeding sites (Berrill et al. 1997, Howe et al. 1998). Agricultural chemicals may be reducing the quality of wetland habitats adjacent to tilled fields (Hanson et al. 1994, Freemark and Boutin 1995). In addition, sublethal effects of these stressors may make individuals more susceptible to other pathogens (Kiesecker and Blaustein 1997a).

Amphibians may be vulnerable to habitat fragmentation because of their complex life history patterns and metapopulation dynamics (Mann et al. 1991, Vos and Stumpel 1995, Delis et al. 1996, Marsh and Pearman 1997, Gibbs 1998b, Hager 1998, Vos and Chardon 1998, Lehtinen et al. 1999). Fragmentation of these stressors may contribute to amphibian population declines, especially in the Midwest where agriculture dominates the landscape. Draining and filling of wetlands has fragmented wetland habitats and changed the distribution and quality of wetlands in agricultural landscapes (Galatowitsch and van der Valk 1994). The dispersal patterns of amphibians are likely to be influenced by habitat quality and distance between available breeding patches (Dodd and Cade 1998, Gibbs 1998a). A highly fragmented landscape increases the extinction probabilities of local metapopulations (Blaustein et al. 1994). Exotic species introductions have also been blamed for local impacts on amphibian pop-

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ulations (Kats et al. 1988, Werner and McPeck 1994, Kiesecker and Blaustein 1997b, Kupferberg 1997, Lannoo 1998).

Frog and toad surveys in Wisconsin and Iowa have been ongoing for over 10 years (Hemesath 1998, Mossman et al. 1998). These surveys provide a unique opportunity to examine anuran habitat associations using quantitative data. We examined landscape habitat associations of anuran species in Iowa and Wisconsin and tested whether our data support or refute previous anuran habitat classifications. We make recommendations regarding anuran species as bioindicators of wetland habitat quality. We also identified which species shared similar habitat associations and determined whether those associations were consistent across large geographic areas (states).

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 species relative abundance at each survey point. 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 training tapes and specific protocols regarding data collection and recording. All surveys were conducted at night. Anurans 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 (see Appendix A for list of species). 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, 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 their 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 1991–95. 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, were within the range for each species (Christiansen and Bailey 1991, Casper 1996, Mossman et al. 1998), and were ≥ 2000 m apart. Survey locations were distributed across both states ($n = 118$ in Iowa, $n = 260$ in Wisconsin).

Landscape Variables

The anuran survey points were located on and digitized from USGS 7.5 minute quadrangle maps. A circle of radius 1000 m around each survey point was determined to be the smallest size 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 and 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 and Cohen 1995). The area therefore represents a reasonable area of landscape influence, from a metapopulation perspective.

Several geographical information system (GIS) data sets were used to obtain the landscape habitat 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 (1981–92) National Wetland Inventory (NWI) (<http://www.nwi.fws.gov>; Cowardin et al. 1979, Wilen and Bates 1995). Maps for Wisconsin were obtained from the Wisconsin Wetland Inventory (WWI) (Wisconsin Department of Natural Resources 1984–96; scale = 1:24,000) and the Wisconsin hydrology coverages (U.S. Geological Survey 1987–96; scale = 1:100,000). U.S. Geological Survey (1986) land use and land cover (LULC; scale = 1:250,000) maps 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 1).

We used the FRAGSTATS spatial pattern analysis (McGarigal and Marks 1994) software to calculate several landscape metrics for each area (Table 1). 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 habitat variables used in the analysis were grouped into composition, diversity/edge, and patch variables (Table 1).

Statistics

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. Principal components (PC) analysis (SAS Institute Inc. 1990) was used to generalize the individual habitat variables into a smaller number of components, which were named based on their correlations with individual variables. The principal axis method was used to extract the components, and this was followed by a varimax (orthogonal) rotation. PC analysis is useful because it can simplify multivariate data sets. Step-wise logistic regression was used to assess the relationship between abundance classes for each species and the individual habitat variables. A second logistic regression analysis examined the relationship between each species and the PC's. A significance level of $P < 0.3$ for the Wald chi-square statistic was required for a variable to enter the model and a level of $P < 0.15$ to remain in the model. If the null hypothesis under the score test for the proportional odds assumption was rejected ($P < 0.05$), abundance classes were merged until the test failed to reject.

Cluster analysis was used to create tree diagrams of associations among those species identified at more than 30 sites. Ward's minimum variance method was applied to standardized maximum abundances of each species at all survey points (SAS Institute Inc. 1990). The cluster analysis shows species relationships based on co-occurrence, while the regressions show how species are related to habitat variables. These two measures of association give different perspectives on how species are related to each other and to the landscape. Cluster analysis may also be useful for identifying groups of species that would benefit from similar management.

Habitat Classifications

Our data were compared with general habitat associations published by the Minnesota Department of Natural Resources (1997). In that publication, the authors classified *Pseudacris crucifer*, *Bufo americanus*, *Rana sylvatica*, and *Hyla versicolor* as forest species; *R. catesbeiana*, *Acris crepitans*, *R. clamitans*, *R. palustris*, and *R. septentrionalis* as lake or stream species; and *B. cognatus*, *R. pipiens*, *P. triseriata*, and *H. chrysocheilus* as grassland species. *Bufo woodhousii* has a similar range in Iowa as *B. cognatus*, and we considered it a grassland species (Christiansen and Bailey 1991). We evaluated how our data supported or failed to support these general habitat classifications. We expected

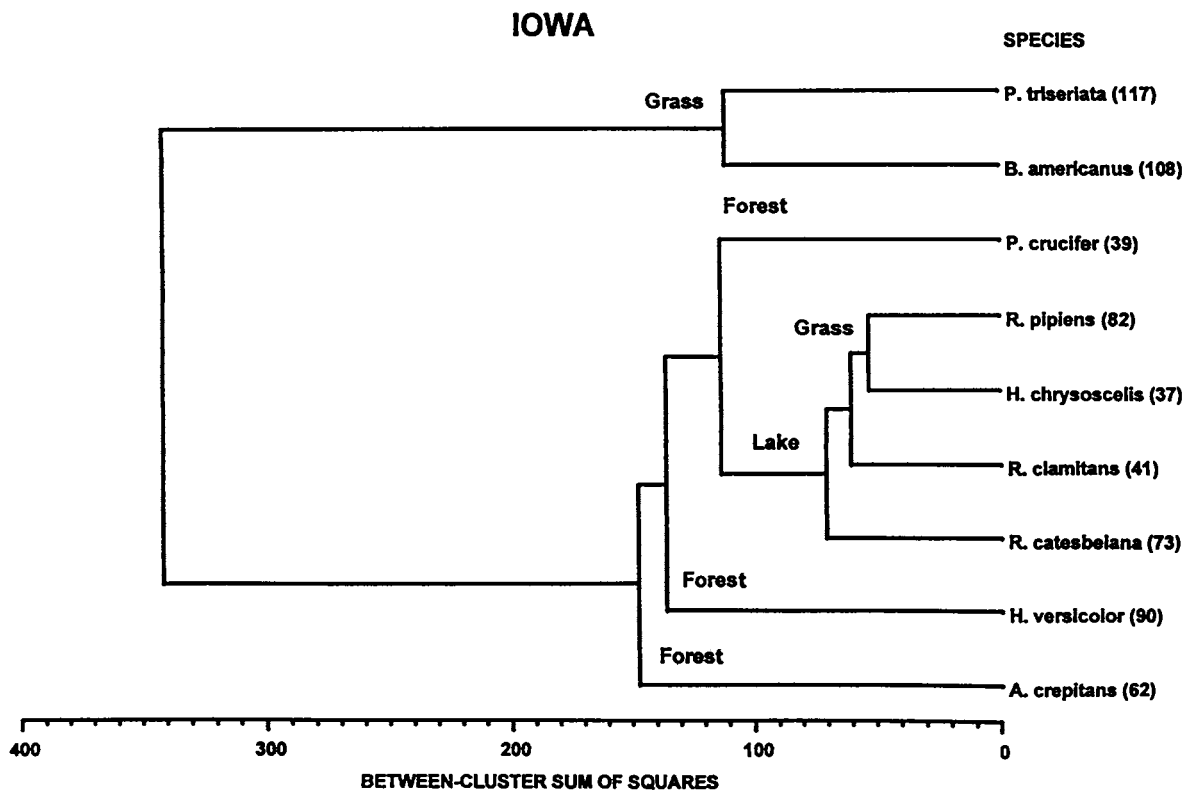
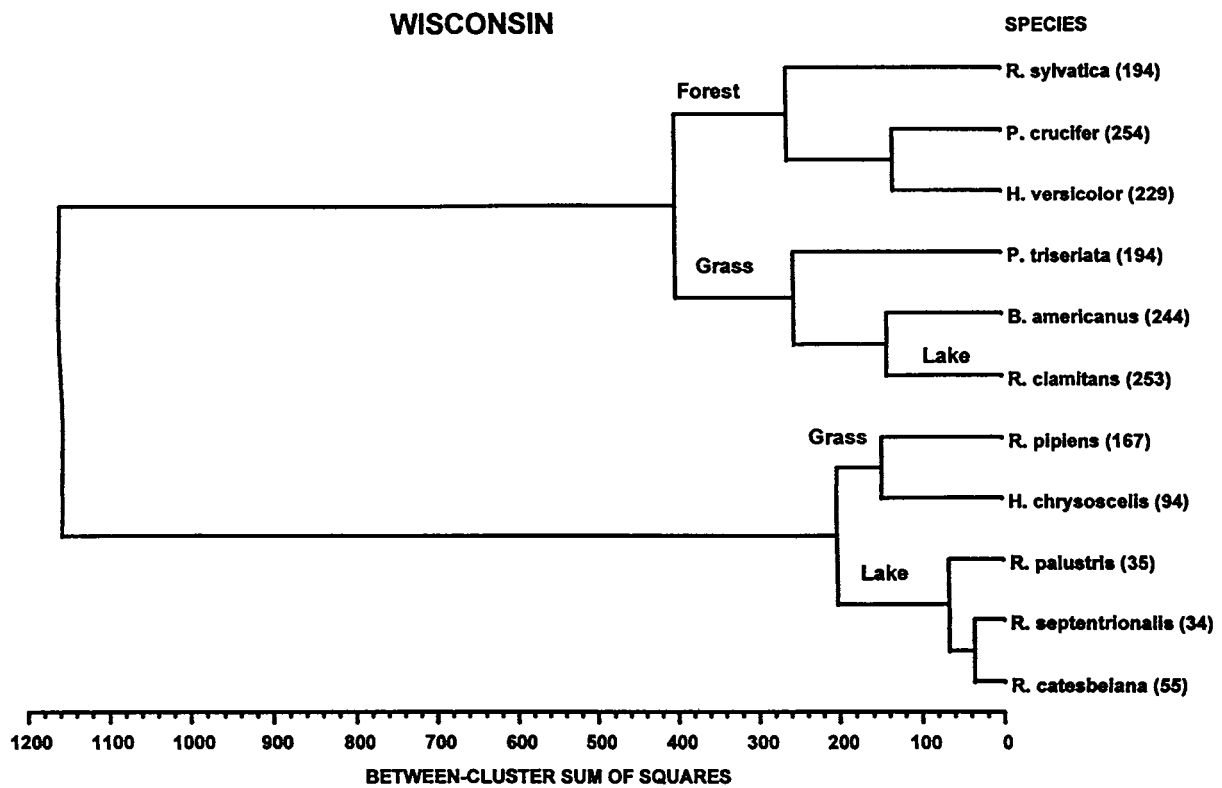


Fig. 1. Tree diagram of associations among species for Wisconsin and Iowa, based on standardized maximum abundances of each species at all survey points. Number of points where the species was observed is given in parentheses, general habitat associations derived from our data are indicated on the diagram.

Table 1. Landscape variables used in the analysis. Descriptions refer to characteristics of the 1000 m radius buffer surrounding each survey point.

Variable Type	Acronym	General Habitat	Description (area in m ² , length in m)
Composition	FOCA	Forest	Area of forest (deciduous, evergreen, mixed)
	AGCA	Grass	Area of agricultural land (cropland, pasture, orchards, other agricultural land)
	URCA		Presence or absence of urban land (residential, commercial, industrial, transportation)
	WACA	Lake	Area of water (lakes, rivers, reservoirs)
	WEMCA	Grass	Area of wetland-emergent vegetation
	WFOCA	Forest	Area of wetland-forest/shrub
	NPERMLAR		Area of non-permanent wetlands
	PERMLAR	Lake	Area of permanent wetlands
	WET_M		Length of all wetlands mapped as lines (Iowa only)
	WET_CT		Number of all wetlands mapped as points
Diversity/edge	WEMED	Grass	Edge density (m of edge/ha) of wetland-emergent
	WFOED	Forest	Edge density (m of edge/ha) of wetland-forest/shrub
	EDGFO	Forest	Total length of edge between forest and all wetland types, including water
	EDGAG	Grass	Total length of edge between agricultural and all wetland types, including water
	EDGUR		Presence or absence of edge between urban and all wetland types, including water
	SHDI		Shannon diversity of patch types/area (index of patch diversity)
Patch	WEMAW	Grass	Area-weighted mean patch fractal dimension of wetland-emergent (highly convoluted patches)
	WFOAW	Forest	Area-weighted mean patch fractal dimension of wetland-forest/shrub (highly convoluted patches)
Principal Components	FORESTED WETLAND	Forest	Dominated by forested wetland cover types and edges (WFOCA, NPERMLAR, and WFOED)
	UPLAND FOREST	Forest	Dominated by upland forest cover types and edges (FOCA, EDGFO)
	EMERGENT WETLAND	Grass	Dominated by emergent wetland cover types and edges (WEMCA, WEMED, EDGAG, and WEMAW)
	LAKE URBAN	Lake	Dominated by water cover types and edges (WACA, PERMLAR) Dominated by urban cover types and edges (URCA, EDGUR)

to find positive associations between the forest species identified above and our forest variables (FOCA, WFOCA, WFOED, EDGFO, WFOAW, FORESTED WETLAND, and UPLAND FOREST, see Table 1 for definitions). Similarly, we expected to find positive associations between the lake, stream, and river species identified above and our water variables (WACA, PERMLAR, and LAKE). Finally, we expected positive associations between the grassland species identified above and our agriculture and emergent wetland variables (AGCA, WEMCA, WEMED, EDGAG, WEMAW, and EMERGENT WETLAND). We used the sign test (Zar 1984) to examine whether single habitat associations were significant among species.

RESULTS

Data were obtained for 118 survey locations in Iowa and 260 in Wisconsin. If a species' range did not cover the entire state, the number of survey locations for that species was less than the total number of survey locations in the state. The first five components (Table 1) in the PC analysis explained 75% of the variance in the habitat data. Logistic regressions were significant for 12 species in

each state (Appendix A); landscape habitat associations were summarized for 14 species of anurans, including both states (Table 2). *Bufo cognatus* and *B. woodhousii* were found only in Iowa, while *R. septentrionalis* and *R. sylvatica* were found only in Wisconsin.

Cluster analysis tree diagrams of species associations between states showed some similarities, but also some differences (Fig. 1). *Pseudacris crucifer* and *H. versicolor* have a close association in both states, as do *P. triseriata* and *B. americanus*, and *R. pipiens* and *H. chrysocheilus*. However, *R. clamitans* and *R. catesbeiana* were associated with different species in each state.

Every species had at least one positive or negative association with one of the habitat variables. Our data supported the general habitat associations identified by the Minnesota Department of Natural Resources (1997) for the forest species *H. versicolor*, *P. crucifer*, *R. sylvatica* and the grassland species *H. chrysocheilus*, *R. pipiens*, and *P. triseriata* (Table 2).

Our data provided some support for the predicted general landscape habitat associations of lake and stream species *R. catesbeiana*, *R. clamitans*, *R. palustris*, and *R. septentrionalis*, but the relationships

Table 2. Significant habitat variables in logistic regression models of species abundance classes for Iowa (I) and Wisconsin (W). Species names are abbreviated as follows: Ba (*Bufo americanus*), Bc (*B. cognatus*), Bw (*B. woodhousii*), Ac (*Acris crepitans*), Hc (*Hyla chrysoscelis*), Hv (*H. versicolor*), Pc (*Pseudacris crucifer*), Pt (*P. triseriata*), Rca (*Rana catesbeiana*), Rcl (*R. clamitans*), Rpa (*R. palustris*), Rpi (*R. pipiens*), Rse (*R. septentrionalis*), Rsy (*R. sylvatica*).

Species	Ba		Bc		Bw		Ac		Hc		Hv	
Habitat*	Forest Grass		Grass		Grass		Lake Forest		Grass		Forest	
State	I	W	I	W	I	W	I	W	I	W	I	W
a) Individual**												
FOCA				—		—		P			P	P
AGCA			P	—		—			P			P
URCA				—		—	N				N	
WACA				—		—			N			
WEMCA	P			—		—						
WFOCA				—		—	P		N		P	P
NPERLAR		N		—		—	N					
PERLAR				—		—	N		P			P
WETM	P			—	N	—	N					
WETCT		N		—		—						
WEMED				—		—						
WFOED				—		—						
EDGFO				—		—	P		P			
EDGAG	P	P		—		—	P					
EDGUR	P			—		—			N			N
SHDI				—		—						P
WEMAW				—		—		N		P		
WFOAW	N	P		—		—						
b) Principal Components**												
FORESTED												
WETLAND			P	—		—			N			P
UPLAND												
FOREST		N		—		—			N		P	P
EMERGENT												
WETLAND	P	P		—		—		N		P	N	
LAKE				—		—						P
URBAN				—	P	—		N	N		N	N

*Predicted general habitat associations (Minnesota Department of Natural Resources 1997). When our data contradicted the expected association, our habitats are shown in italics. Bold print indicates support for the predicted associations, underlining indicates weaker support, and plain text indicates our data failed to support predicted habitat associations.

**Habitat variables that contributed to the logistic regression model are shown as P (positive) or N (negative) in their association with anuran species. A (—) indicates no data available because that species was not present within that state. Bold print indicates relationships in the expected direction, based on predicted habitat associations. See Appendix A for details of the regression models.

were less consistent. These species were associated with lake habitats, but they were also associated with other habitat types. In some cases, the associations were not the same in both states. *Rana catesbeiana* and *R. septentrionalis* were associated with both lake and forest habitats. *Rana palustris* was associated with lakes in Iowa and forests, wetlands, and agriculture in Wisconsin. *Rana clamitans* was associated with lake variables only in Wisconsin.

The data failed to support predicted landscape habitat associations for *B. americanus*, *B. cognatus*, *B. woodhousii*, and *A. crepitans*. *Bufo americanus* had positive associations with grassland variables, not forest variables, as predicted. Similarly, *A. crepitans* had closer associations with forests than with lakes, again contradicting the predicted association. Our analysis has limited value for predicting landscape habitat associations for *B. cognatus* and *B. woodhousii*. These species had few positive associations, none of which were our grassland var-

iables. The species were observed at only 7 of 32 and 12 of 58 sites, respectively, within the range of these species.

Of all the habitat variables, only the PC URBAN meets the sign test criteria ($P < 0.05$) for significant association among all species. Significant negative associations with URBAN occurred for 10 of 11 species. The other PC's had more positive than negative associations across all species, but the ratios did not meet the test for significance. Patch diversity (SHDI) was positive for six species and negative for one.

DISCUSSION

The common species in each state [Wisconsin: *P. crucifer* (forest), *H. versicolor* (forest), *B. americanus* (grass), and *R. clamitans* (lake); Iowa: *P. triseriata* (grass) and *B. americanus* (grass)] reflect the domi-

one of the most widely distributed anurans in Wisconsin (Mossman et al. 1998). *Rana clamitans* was also the most common species found in southern Ontario (Hecnar and M'Closkey 1997). *Rana clamitans* was associated with permanent water bodies and forests in Quebec (Bonin et al. 1997). Others have shown that *R. clamitans* is widely distributed among many types of wetlands, from permanent to temporary (Werner and McPeck 1994). Of the other lake and stream species, *R. catesbeiana* has been widely introduced into water bodies (Lannoo 1996), changing its natural distribution pattern. *Rana septentrionalis* has a restricted, boreal distribution (Casper 1996) and *R. palustris* had inconsistent landscape habitat associations, being associated with lake variables in Iowa and forest, agriculture, lake, and patch diversity variables in Wisconsin. However, given the association of *R. palustris* with cold water streams and high quality wetlands (Vogt 1981), primarily in the Driftless Area ecoregion of western Wisconsin, northeastern Iowa, and southeastern Minnesota, it could be considered a biotic indicator for cold water wetland habitats such as forested streams and spring-fed wetlands. Concerns over *R. palustris* populations in three states (Oldfield and Moriarty 1994, Hemesath 1998, Mossman et al. 1998) indicate that it is likely sensitive to environmental stressors. Vogt (1981) warned that *R. palustris* is sensitive to changes in water quality (requiring cold water for breeding) and has been historically rare in Wisconsin.

Landscape habitat associations and community relationships for some species varied between the states. Others have also found that amphibian community associations differ among regions. Hecnar and M'Closkey (1997) used methods different from ours to examine community associations among amphibians in Ontario, Canada. Except for the forest triad of *R. sylvatica*, *H. versicolor*, and *P. crucifer*, the species associations they found are not the same as the ones we identified. Furthermore, Hecnar and M'Closkey's (1997) associations do not match those of amphibians in Michigan (Collins and Wilbur 1979). Why do anuran species associations within a community show different patterns from one region to another? Limiting resources may vary from one landscape to another; competitive or predatory factors (fish or *R. catesbeiana* depredation) may be more severe in certain locations (Kats et al. 1988, Werner and McPeck 1994). The implication is that one habitat management prescription for a species may not be appropriate in all locations if habitat preferences and ecological community companions change across space or time.

It is necessary to understand how community relationships are structured and what limits populations before effective management can be applied. We found that *R. pipiens*, *R. clamitans* and *H. chrysoscelis* in Iowa frequently co-occur with *R. catesbeiana*, based on the cluster analysis. Does this affect their populations? *Rana pipiens* and *H. chrysoscelis* populations have experienced declines in Iowa (Hemesath 1998), whereas *R. clamitans* populations have remained stable, perhaps because the larvae of this species are unpalatable to predatory fish (Kats et al. 1988). When predators, such as *R. catesbeiana* are introduced widely into new habitats, it could affect species assemblages (Lannoo 1996). At present, *R. catesbeiana* has been distributed more widely for aquaculture in Iowa than in Wisconsin (M. Lannoo, pers. comm.; B. Hay, pers. comm.) and this may explain some of the differences we observed between the states. Werner and McPeck (1994) experimentally demonstrated that predator effects differ between populations of *R. catesbeiana* and *R. clamitans*.

Habitat associations may be helpful in identifying differences in habitat preferences among closely-related species, or in identifying species that could be at risk from changes in land use or management practices. For example, *H. versicolor* and *H. chrysoscelis* have differences in habitat preference consistent across the two states. *Hyla versicolor* is more closely associated with forest cover than *H. chrysoscelis*. This matches the differences in habitat preferences identified by Vogt (1981) and Oldfield and Moriarty (1994) who describe *H. chrysoscelis*

as a prairie or oak savanna species and *H. versicolor* as a woodland species. Because the calls of the species are similar and can vary with temperature, the accuracy of observer records has been questioned (Hemesath 1998). It appears that many of our observers distinguished these species accurately; if they had not, we would detect few differences in landscape habitat associations.

A species of immediate concern in the Upper Midwest is *A. crepitans*. It has virtually disappeared from Minnesota (Oldfield and Moriarty 1994), northern Iowa (Hemesath 1998), and most of Wisconsin (Casper 1996, Mossman et al. 1998). Our data indicate positive landscape-scale associations with forest cover and forest edges and a negative association with urban variables in both states. Sample sizes in Wisconsin were too low (8 sites) to make strong interpretations of the data. Based on the Iowa cluster analysis, *A. crepitans* is most frequently found with *H. versicolor*. Jung (1993) observed that *A. crepitans* most frequently shares habitats with *R. clamitans* in southwestern Wisconsin. Hay (1998) suggests that factors such as climate change, a short life span, and microhabitat changes in pond bank vegetation may have contributed to *A. crepitans* declines. Lannoo (1998) proposes that the cumulative effects of stressors, such as drought and a higher incidence of predators in breeding ponds are likely factors leading to *A. crepitans* declines.

Habitat changes alone seem unsatisfactory as an explanation for the precipitous population declines of *A. crepitans*, once a common species. The species appears to have experienced not only a range contraction, but a shift in habitat associations away from more open habitats (as reported in historical accounts) toward more forested habitats (our data), at least in Iowa. Could contaminant effects be influencing both of these patterns? Declines began after 1950 (Hay 1998), a time when agricultural chemicals came into wide use. Open grassland habitats have largely been converted to intensive row-crop agriculture or are adjacent to intensive agriculture, where herbicides and pesticides are widely used. Forested habitats are presumably less directly affected by these chemicals and could serve as refugia or corridors for movement. Contaminants can produce direct mortality, delay metamorphosis, or affect neurological functioning and predator avoidance behavior (Diana and Beasley 1998). Small delays in metamorphosis would stress populations, since *A. crepitans* breeds late in the summer and juveniles must accumulate nutrient reserves before winter. These effects would be most pronounced in northern populations, where winters arrive earlier and are more severe. Conversely, a contaminant could be distributed in a pattern that correlates with *A. crepitans* declines because of the biogeochemical properties of the soil, distribution of point sources, or patterns of agricultural application, etc. Other amphibian species exhibit adverse responses to agricultural chemicals. *Rana pipiens* and *B. americanus* larvae were found to be more sensitive than fish species to atrazine and alachlor, two commonly used agricultural chemicals (Howe et al. 1996). It is notable that contaminant effects on amphibians at the population level have rarely been demonstrated, despite proven laboratory effects (Hecnar 1995, Russell et al. 1995) and predicted amphibian vulnerability due to permeable skin, complex life cycles, and close associations with polluted wetlands [but see Fashingbauer (1957) concerning DDT effects on *R. sylvatica*]. The possibility that *A. crepitans* has some unrecognized vulnerability to a contaminant deserves more attention.

Urban environments present a number of hazards for amphibians. Conversion of wetland habitats to other uses, proliferation of roads, urban predators, and contaminant run-off from lawns and industrial areas are all potential problems for amphibian populations. The hazards of an urban environment for anurans have been discussed in depth elsewhere (Fahrig et al. 1995, Ashley and Robinson 1996, Spellerberg 1998, Knutson et al. 1999). Some species may be more affected by urban development than others, due to life history or

behavioral characteristics that increase their vulnerability. For example, species that migrate between different habitats are at higher risk from road mortality than species that remain in a single habitat. The negative association of *P. crucifer* with urban habitats supports the hypothesis that urbanization may be contributing to its population decline in Wisconsin (Mossman et al. 1998). Urbanization should be considered a potential stressor in any investigation of amphibian population declines and may be a serious problem in states with a high proportion of developed land.

Landscape patch diversity (SHDI) is a measure of interspersions or fragmentation of habitat patches within the buffer surrounding the survey point. Our finding that many anuran species are positively associated with patch diversity is in accord with the findings of Mann et al. (1991) who found that the probability of species occupancy increased as the number of breeding pools increased and Vos and Stumpel (1995) who found that pond density was higher surrounding occupied vs. unoccupied ponds. Interspersion of different habitat types may increase breeding opportunities and increase the probability of at least one site being suitable. Interspersion of habitat patches could also affect anuran dispersal ability. Hecnar and M'Closkey (1997) found a positive relationship between good dispersal abilities and high incidence. Our data fail to support this relationship. *Hyla versicolor*, with one of the lowest reported maximum dispersal distances (Hecnar and M'Closkey 1997), was one of the most common species in Wisconsin. The same was true for *P. triseriata* in Iowa.

Hager (1998) applied island biogeography theory to amphibian communities and found that *H. versicolor* was not present on small islands in the Great Lakes, indicating that the species was area-sensitive. We cannot compare our data directly, but if *H. versicolor* is area-sensitive, we would expect to find a negative association between *H. versicolor* and patch diversity or one of the edge measures. We found instead a positive association with patch diversity and a negative association with urban edges in Wisconsin.

Limitations of our study included non-random selection of survey points (Mossman et al. 1998), landscape data of varying ages, and lack of experimental manipulations of land cover. Therefore, our regression analyses should be viewed as exploratory. Despite these limitations, we have refined our knowledge of habitat associations for anurans in the upper Midwest and identified some potential risk factors. Improvements in both anuran survey techniques and the availability of current GIS maps across large geographic regions will increase our ability to define and test specific landscape habitat associations for anuran species.

Management Implications

We suggest that *R. sylvatica*, *H. versicolor*, and *P. crucifer* be further investigated as bioindicators of forest health, *R. pipiens* and *P. triseriata* as bioindicators of grassland health, and *R. palustris* as a bioindicator of cold water wetlands. For example, these species are likely candidates to be included in monitoring efforts designed to detect declines in ecosystem health in the Midwest. Managers should seek to improve the quality of forest, grassland, and cold water wetland ecosystems in the Upper Midwest for amphibians, given concerns about *P. crucifer*, *R. pipiens*, and *R. palustris* populations in one or both states. This means conserving and enhancing existing wetland complexes with an interspersion of different habitat types, ideal breeding habitats for many anurans. Efforts should be made to restore wetlands where they have been lost. Care should be taken to avoid unnecessary introduction of predators on amphibian larvae (fish and *R. catesbeiana*) into wetland systems. More information is needed on specific risk factors for amphibians living in urban environments. Land use planners should consider the potential negative effects on amphibian pop-

ulations of urban sprawl and seek to minimize threats to these populations. We suggest contaminants deserve more investigation regarding the abrupt and widespread declines of *A. crepitans*.

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Appendix A. Results of the logistic regression of species abundance classes with the landscape variables for Iowa and Wisconsin. The -2 log likelihood statistic has a chi-square distribution under the null hypothesis that all regression coefficients of the model are 0. The standardized parameter estimates give the standardized estimated coefficients of the fitted logistic regression model. The $P > \text{Chi-square}$ is the p-value of the Wald chi-square for individual variables in the model. The odds ratio is the amount by which the variable increases the odds of observing the species. The predicted probability is the percentage of concordant and discordant observation pairs, given the model.

Scientific name	<i>n</i>	Individual variables*	Model -2 Log L $P > \text{Chisq}$	Std. Param. Est.	$P > \text{Chisq}$	Odds ratio	Predicted probability	Principal component factors*	Model -2 Log L $P > \text{Chisq}$	Std. Param. Est.	$P > \text{Chisq}$	Odds ratio	Predicted Probability	
IOWA														
<i>Bufo americanus</i>	118	WEMCA	0.0001	0.276	0.0316	1.033	Con = 71.1% Dis = 28.5%	EMERG WETL	0.0019	0.306	0.0040	1.740	Con = 60.4% Dis = 39.0%	
		WFOAW		-0.334	0.0018	0.398								
		WET_M		0.296	0.0061	1.000								
		EDGAG		0.181	0.1494	1.000								
		EDGUR		0.263	0.0127	3.645								
<i>Bufo cognatus</i>	32	AGCA	0.0969	0.505	0.1550	1.017	Con = 68.0% Dis = 32.0%	FOR WETL	0.1423	0.418	0.1883	12.268	Con = 61.1% Dis = 38.9%	
<i>Bufo woodhousii</i>	58	WET_M	0.0966	-0.357	0.1360	1.000	Con = 72.1% Dis = 22.5%	URBAN	0.1367	0.244	0.1276	1.586	Con = 72.6% Dis = 24.5%	
<i>Acris crepitans</i>	118	URCA	0.0002	-0.370	0.0047	0.195	Con = 75.9% Dis = 23.8%	None significant						
		WFOCA		1.065	0.0338	1.080								
		WET_M		-0.397	0.0049	1.000								
		PERM_AR		-0.483	0.0033	1.000								
		NPERM_AR		-1.401	0.0131	1.000								
		EDGFO		0.375	0.0069	1.000								
		EDGAG		0.742	0.0003	1.000								
<i>Hyla chrysoscelis</i>	118	EDGFO	0.0497	0.218	0.0484	1.000	Con = 50.2% Dis = 30.1%	URBAN	0.1344	-0.185	0.1596	0.715	Con = 55.6% Dis = 41.1%	
		EDGUR		-0.216	0.1274	0.346								
<i>Hyla versicolor</i>	118	FOCA	0.0001	0.404	0.0005	1.013	Con = 68.6% Dis = 25.5%	UPL FOR EMERG WETL URBAN	0.0001	0.366	0.0009	1.964	Con = 72.3% Dis = 27.4%	
		URCA		-0.338	0.0012	0.224								
		WFOCA		0.160	0.1392	1.012								
<i>Pseudacris crucifer</i>	118	FOCA	0.0001	0.614	0.0001	1.020	Con = 74.6% Dis = 17.4%	UPL FOR EMERG WETL URBAN	0.0001	0.478	0.0001	2.411	Con = 76.7% Dis = 22.9%	
		EDGUR		-0.353	0.0438	0.176								
<i>Pseudacris triseriata</i>	118	FOCA	0.0001	-0.163	0.1261	0.995	Con = 73.0% Dis = 26.7%	UPL FOR EMERG WETL	0.0004	-0.347	0.0008	0.528	Con = 68.3% Dis = 31.3%	
		WEMED		0.323	0.0319	1.061								
		WEMAW		0.221	0.0335	2.613								
		WET_M		-0.272	0.0116	1.000								
		WET_CT		-0.216	0.0393	0.800								
<i>Rana catesbeiana</i>	118	WACA	0.0003	-0.312	0.0249	0.982	Con = 63.4% Dis = 34.5%	FOR WETL EMERG WETL LAKE URBAN	0.0016	0.224	0.0191	1.506	Con = 64% Dis = 34.5%	
		NPERM_AR		0.157	0.1377	1.000								
		EDGAG		0.336	0.0039	1.000								

Appendix A. Continued.

Scientific name	n	Individual variables*	Model -2 Log L P > Chisq	Std. Param. Est.	P > Chisq	Odds ratio	Predicted probability	Principal component factors*	Model -2 Log L P>Chisq	Std. Param. Est.	P> Chisq	Odds ratio	Predicted Probability
<i>Rana clamitans</i>	57	URCA WFOCA NPERMLAR	0.0301	-0.219 -1.170 1.413	0.1326 0.0690 0.0312	0.368 0.938 1.000	Con = 71.6% Dis = 27.8%	NONE SIGNIFICANT					
<i>Rana palustris</i>	56	WACA	0.0012	0.802	0.0148	1.068	Con = 68.3% Dis = 26.0%	LAKE	0.0023	0.716	0.0226	4.971	Con = 70.7% Dis = 27.7%
<i>Rana pipiens</i>	118	URCA WFOED	0.0002	-0.326 0.261	0.0017 0.0072	0.236 1.038	Con = 62.4% Dis = 26.5%	FOR WETL EMERG WETL URBAN	0.0049	0.190 0.174 -0.215	0.0455 0.0660 0.0304	1.415 1.371 0.677	Con = 65.7% Dis = 32.1%
WISCONSIN													
<i>Bufo americanus</i>	260	WFOAW WET_CT NPERMLAR EDGAG	0.0005	0.179 -0.267 -0.228 0.295	0.1047 0.0031 0.0228 0.0372	2.063 0.933 1.000 1.000	Con = 71.8% Dis = 27.3%	EMERG WETL UPL FOR	0.0212	0.269 -0.153	0.0233 0.1235	1.622 0.751	Con = 64.0% Dis = 35.0%
<i>Acris crepitans</i>	142	FOCA WEMAW	0.0001	0.491 -0.555	0.0080 0.0047	1.015 0.152	Con = 82.8% Dis = 12.7%	EMERG WETL URBAN	0.0026	-0.549 -0.548	0.0186 0.1146	0.398 0.351	Con = 81.4% Dis = 15.5%
<i>Hyla chrysoscelis</i>	260	AGCA WACA WFOCA WEMAW PERMLAR	0.0001	0.254 -0.352 -0.187 0.237 0.495	0.0099 0.0035 0.0641 0.0106 0.0001	1.004 0.977 0.993 2.075 1.000	Con = 70.2% Dis = 29.4%	EMERG WETL UPL FOR FOR WETL	0.0001	0.326 -0.172 -0.168	0.0001 0.0286 0.0425	1.800 0.724 0.740	Con = 65.8% Dis = 33.7%
<i>Hyla versicolor</i>	260	FOCA AGCA WFOCA PERMLAR EDGUR SHDI	0.0001	0.909 0.688 0.454 0.258 -0.158 0.259	0.0001 0.0046 0.0001 0.0223 0.0444 0.0069	1.018 1.012 1.018 1.000 0.533 3.566	Con = 74.1% Dis = 25.7%	UPL FOR FOR WETL LAKE URBAN	0.0001	0.358 0.207 0.119 -0.253	0.0001 0.0068 0.0931 0.0004	1.953 1.450 1.241 0.612	Con = 71.6% Dis = 28.2%
<i>Pseudacris crucifer</i>	260	FOCA URCA WFOED WET_CT	0.0001	0.699 -0.166 0.326 -0.317	0.0001 0.0499 0.0016 0.0004	1.014 0.535 1.036 0.921	Con = 81.0% Dis = 18.7%	UPL FOR LAKE URBAN	0.0001	0.531 0.207 -0.382	0.0001 0.0176 0.0001	2.702 1.458 0.475	Con = 78.0% Dis = 21.8%
<i>Pseudacris triseriata</i>	260	FOCA WEMED WFOAW NPERMLAR EDGFO SHDI	0.0001	-0.212 0.364 -0.163 -0.237 0.156 -0.163	0.0235 0.0001 0.0260 0.0028 0.0990 0.0392	0.996 1.069 0.518 1.000 1.000 0.449	Con = 68.3% Dis = 31.4%	EMERG WETL UPL FOR FOR WETL	0.0001	0.235 -0.178 -0.236	0.0004 0.0057 0.0004	1.526 0.717 0.655	Con = 66.3% Dis = 33.3%

Appendix A. Continued.

Scientific name	n	Individual variables*	Model -2 Log L P > Chisq	Std. Param. Est.	P > Chisq	Odds ratio	Predicted probability	Principal component factors*	Model -2 Log L P>Chisq	Std. Param. Est.	P> Chisq	Odds ratio	Predicted Probability
<i>Rana catesbeiana</i>	260	AGCA	0.0001	-0.902	0.0008	0.984	Con = 87.4% Dis = 11.1%	UPL FOR LAKE	0.0001	0.428 0.550	0.0001	2.230 2.728	Con = 81.4% Dis = 17.4%
		WEMCA		-0.412	0.0106	0.966							
		WFOED		-0.752	0.0006	0.921							
		NPERMLAR		-0.252	0.1351	1.000							
		EDGFO		0.753	0.0001	1.000							
		EDGAG		0.507	0.0136	1.000							
		SHDI		0.770	0.0001	43.914							
<i>Rana clamitans</i>	260	WEMCA	0.0001	0.173	0.0890	1.015	Con = 66.0% Dis = 33.6%	LAKE URBAN	0.0166	0.121 -0.164	0.0963 0.0174	1.247 0.727	Con = 59.6% Dis = 39.8%
		WET_CT		-0.231	0.0007	0.942							
		EDGAG		-0.183	0.0178	1.000							
		SHDI		0.145	0.0633	2.036							
<i>Rana palustris</i>	260	FOCA	0.0001	4.066	0.0055	1.084	Con = 82.6% Dis = 16.7%	UPL FOR URBAN	0.0002	-0.396 -0.375	0.0011 0.0074	0.477 0.482	Con = 71.0% Dis = 27.2%
		AGCA		4.415	0.0080	1.081							
		WFOCA		0.768	0.0107	1.030							
		WFOAW		-0.241	0.0280	0.376							
		PERMLAR		1.433	0.0524	1.000							
		NPERMLAR		1.141	0.0985	1.000							
		EDGFO		-0.855	0.0013	1.000							
		SHDI		0.694	0.0004	30.114							
<i>Rana pipiens</i>	260	AGCA	0.0001	0.367	0.0001	1.006	Con = 70.3% Dis = 29.3%	EMERG WETL UPL FOR LAKE	0.0001	0.323 -0.285 0.241	0.0001	1.787 0.587 1.552	Con = 68.2% Dis = 31.3%
		WEMCA		0.133	0.0982	1.011							
		WFOAW		-0.144	0.0375	0.559							
		PERMLAR		0.296	0.0008	1.000							
		SHDI		0.261	0.0024	3.603							
<i>Rana septentrionalis</i>	108	FOCA	0.0002	0.900	0.0051	1.019	Con = 73.8% Dis = 24.8%	UPL FOR LAKE	0.0040	0.435 0.222	0.0048 0.0877	2.505 1.466	Con = 65.9% Dis = 32.4%
		WET_CT		0.205	0.0724	1.044							
		SHDI		0.862	0.0006	104.082							
<i>Rana sylvatica</i>	260	FOCA	0.0001	0.207	0.0083	1.004	Con = 75.0% Dis = 24.8%	EMERG WETL UPL FOR FOR WETL	0.0001	-0.162 0.517 0.278	0.0195 0.0001 0.0001	0.747 2.634 1.647	Con = 74.0% Dis = 25.7%
		WEMED		-0.216	0.0048	0.961							
		WFOED		0.347	0.0001	1.039							
		WFOAW		0.321	0.0004	3.660							

*See Table 1 for definitions of variables.