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AGRICULTURAL PONDS SUPPORT AMPHIBIAN POPULATIONS

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Abstract. In some agricultural regions, natural wetlands are scarce, and constructed agricultural ponds may represent important alternative breeding habitats for amphibians. Properly managed, these agricultural ponds may effectively increase the total amount of breeding habitat and help to sustain populations. We studied small, constructed agricultural ponds in southeastern Minnesota to assess their value as amphibian breeding sites. Our study examined habitat factors associated with amphibian reproduction at two spatial scales: the pond and the landscape surrounding the pond. We found that small agricultural ponds in southeastern Minnesota provided breeding habitat for at least 10 species of amphibians. Species richness and multispecies reproductive success were more closely associated with characteristics of the pond (water quality, vegetation, and predators) compared with characteristics of the surrounding landscape, but individual species were associated with both pond and landscape variables. Ponds surrounded by row crops had similar species richness and reproductive success compared with natural wetlands and ponds surrounded by nongrazed pasture. Ponds used for watering livestock had elevated concentrations of phosphorus, higher turbidity, and a trend toward reduced amphibian reproductive success. Species richness was highest in small ponds, ponds with lower total nitrogen concentrations, tiger salamanders (*Ambystoma tigrinum*) present, and lacking fish. Multispecies reproductive success was best in ponds with lower total nitrogen concentrations, less emergent vegetation, and lacking fish. Habitat factors associated with higher reproductive success varied among individual species. We conclude that small, constructed farm ponds, properly managed, may help sustain amphibian populations in landscapes where natural wetland habitat is rare. We recommend management actions such as limiting livestock access to the pond to improve water quality, reducing nitrogen input, and avoiding the introduction of fish.

Key words: agricultural pond; agriculture; amphibian; Driftless Area Ecoregion (Minnesota, USA); farm pond; fish; habitat management; landscape; livestock grazing; nitrogen; stock pond; water quality.

INTRODUCTION

Agriculture strongly dominates the landscapes of some regions of North America, especially the midwestern United States, and agricultural practices have a potentially large influence on amphibian populations because of the attendant problems of habitat loss, isolation, and chemical and nutrient contamination (Bishop et al. 1999, Kolozsvary and Swihart 1999, Zampella and Bunnell 2000, Joly et al. 2001). However, in regions where natural wetlands are scarce, constructed agricultural ponds may represent important alternative breeding habitats for amphibians (Baker and Halliday 1999). Properly managed, agricultural ponds may effectively increase the total amount of breeding habitat in a region and help to sustain populations (Meyer-Aurich et al. 1998, Pechmann et al. 2001).

Effective management of amphibian populations in predominantly agricultural landscapes requires an understanding of what factors influence amphibian populations (Knutson et al. 1999, Semlitsch 2000). Global declines in amphibian populations have made amphibian conservation and habitat management a priority for biologists and the public (Houlahan et al. 2000). For example, in the midwestern United States, the formerly common northern cricket frog (*Acris crepitans*) has largely disappeared from its northern range and the causes for this decline are unknown (Hay 1998, Lannoo 1998). The midwestern United States is also an epicenter for the phenomenon of frog malformations, another environmental puzzle demanding a solution (Souter 2000, Johnson et al. 2002, Kiesecker 2002).

Lehtinen et al. (1999) studied amphibian communities in natural wetlands of central and southwestern Minnesota, a region dominated by row crop agriculture. They found that amphibian species richness was lower with greater wetland isolation and road density at all spatial scales, and lower near urban areas. Hecnar and

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PLATE 1. (Left) Natural wetland and (right) agricultural constructed pond in Winona County, Minnesota, USA, July 2001. USGS photos by Andy Kimball (to view in color, see Appendix E).

M'Closkey (1998) studied amphibian communities in Ontario, Canada and found that species richness was correlated with local variables related to fish predation and to regional variables related to forest cover. Knutson et al. (1999, 2000) found that species richness and relative abundance were positively associated with agricultural land use in Wisconsin, but not in Iowa. Few studies of amphibian communities have focused on constructed agricultural ponds (but see Baker and Halliday 1999, Hazell et al. 2001), even though pond construction is a common practice in agricultural regions (Deal et al. 1997). Despite the prevalent grazing practice of allowing livestock to wade in stock and farm ponds, very few studies have examined the influences of grazing and direct livestock access to breeding ponds on amphibian reproduction (Bull et al. 2001, Jansen and Healey 2003).

We studied constructed agricultural ponds and natural ponds (see Plate 1) to better understand habitat factors that support amphibian populations in agricultural landscapes, particularly factors subject to management actions. We examined the following research questions and hypotheses: (1) Are agricultural land uses adjacent to the breeding pond, such as row crops, grazed grassland, and nongrazed grassland related to amphibian reproductive success? We expected that breeding ponds surrounded by row crops (corn or soybeans) and grazing would have lower species richness and poorer amphibian reproductive success compared with natural wetlands and ponds surrounded by nongrazed grassland (Hecnar 1997, Bishop et al. 1999, Knutson et al. 1999). (2) What is the appropriate spatial scale for amphibian habitat management: the landscape surrounding the pond or the pond itself? We expected that species richness and amphibian reproductive success would be most closely associated with pond variables rather than landscape variables (Bonin et al. 1997*a*, Hecnar 1997, Mazerolle and Villard 1999). Furthermore, we expected that features of the landscape nearest to the pond (within 500 m) would be most associated with species richness and amphibian reproductive success. (3) What aspects of pond design or management will improve amphibian breeding habitat quality? We expected that shallow ponds with moderate amounts of vegetative cover, no fish, and at least medium water quality would have higher species richness and reproductive success (Lannoo 1996, 1998).

Study area

Our study ponds were located in Houston and Winona counties in the state of Minnesota, USA. The study area is part of the Driftless Area Ecoregion of southeastern Minnesota, western Wisconsin, and northeastern Iowa (McNab and Avers 1994: Fig. 1). This ecoregion was not covered by ice during the last (Wisconsin) glaciation, a feature that distinguishes it geologically and topographically from other ecoregions in the agricultural Midwest (Mickelson et al. 1982). The landforms are characterized by maturely dissected, upland plateaus with steep bedrock ridges descending to river drainages that flow to the Mississippi River (McNab and Avers 1994). Prior to European settlement, the ecoregion was covered by an oak savanna complex (*Quercus* spp.) of mixed grasslands, with forests in areas protected from fire. Forests today are mixed oak and maple hardwoods and are interspersed with pastures, hay fields, small towns, and cities. Natural wetlands are scarce and found only in the floodplains of rivers and streams; many natural wetlands have been converted to agriculture. Complex topography and erosive soils in the ecoregion support less intensive agriculture than in many parts of the Midwest.

The thousands of constructed agricultural ponds in the ecoregion, designed to prevent soil erosion, represent nearly all the available lentic wetlands and they are potentially significant breeding habitats for amphibians. Most agricultural ponds are privately owned; adjacent land uses include row crops, livestock (pri-

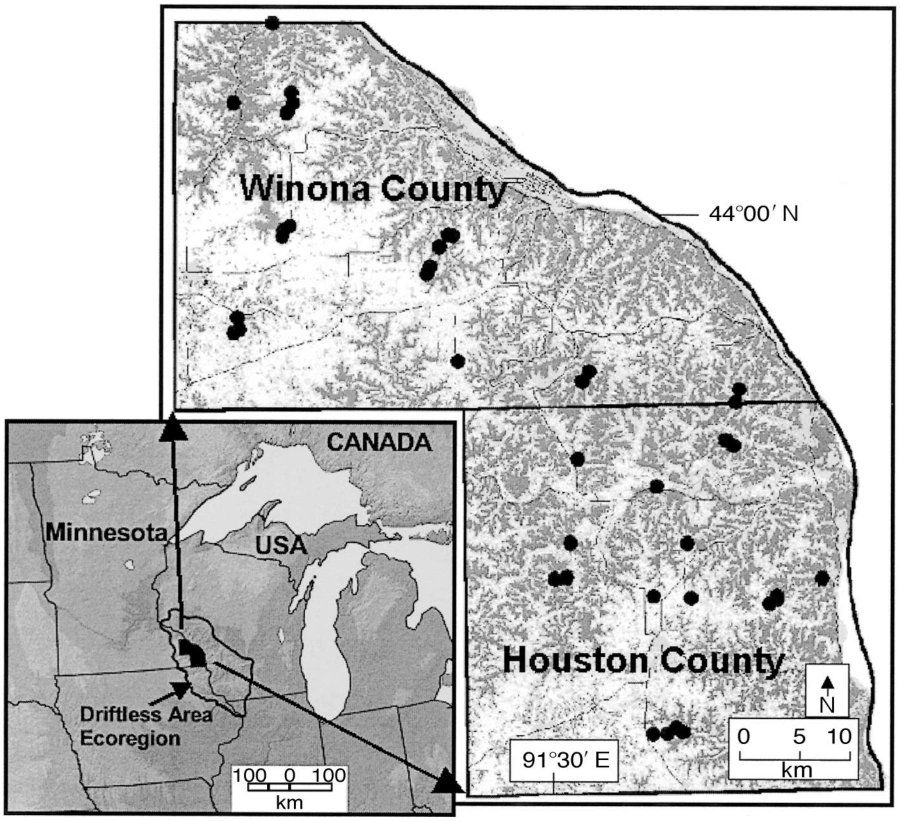

FIG. 1. Map of agricultural pond study sites located in Houston and Winona Counties in southeastern Minnesota, USA.

marily cattle) grazing, and forestry. Some ponds are surrounded by fallow grasslands enrolled in the U.S. Department of Agriculture's Conservation Reserve Program (CRP). To our knowledge, no previous studies have evaluated how constructed agricultural ponds in this ecoregion benefit wildlife.

METHODS

We considered a large number of habitat variables we believed to have potential landscape and environmental effects on amphibians, including land uses adjacent to the breeding pond, pond vegetation and morphometry, water quality, and aquatic predators. We evaluated amphibian habitat variables at two scales (the landscape surrounding the pond and the pond itself) and associated them with amphibian species richness and amphibian reproductive success.

We studied 40 ponds within an agricultural landscape (Fig. 1). Ten ponds were of natural origin (natural) and 30 were constructed (Appendix E). The 30 constructed ponds were further classified based on land uses adjacent to the pond: row crop agriculture (agricultural), grazed grassland (grazed), and nongrazed grassland (nongrazed). If domestic livestock (primarily cattle) had direct access to the pond, it was considered grazed. If the grass buffer surrounding the pond was <30 m wide and adjacent to row crop agriculture (corn or soybeans), the pond was considered agricultural. If the buffer strip was ≥30 m wide and had no livestock grazing, the pond was considered nongrazed. The natural ponds were associated with small streams and rivers. Because of the scarcity of natural ponds, we were unable to control for land uses surrounding them. Ephemeral wetlands and all ponds within 80 m of barnyards or livestock confinement areas were excluded.

We used U.S. Fish and Wildlife Service National Wetland Inventory (NWI) maps (1979–1988, 1:24 000) overlaid on U.S. Geological Survey Digital Orthophoto Quarter Quad maps (DOQQ: 1991 [available online])[5] to identify potential study ponds. Constructed ponds were classified as diked or impounded and natural ponds were classified as palustrine, unconsolidated bottom, and intermittently flooded (Cowardin et al. 1979). Ponds identified on the DOQQ maps but not on the NWI maps (constructed after 1988) were also included in the set of potential study ponds. Most ponds were privately owned; written permits for access were obtained from all landowners and public land managers.

We selected study ponds using a two-stage sampling method. In the first stage, a 10-km grid was randomly placed over Houston and Winona Counties and 10 intersection points were selected at random. In the second

[5] URL: ⟨http://deli.dnr.state.mn.vs/metadata/index_th.html⟩

stage, we randomly selected one pond of each type (natural, agricultural, grazed, and nongrazed) in closest proximity to the intersection point. These four pond types were considered treatments in the statistical analysis, while the 10 intersection points were considered a random effect, acting as a block.

Amphibian measures of reproduction

Measures of reproduction are the most sensitive indicators of habitat quality for wildlife species (Van Horne 1983), so we focused on obtaining evidence of amphibian reproduction in the ponds from April to August in years 2000 and 2001. The littoral zone of each pond was searched for amphibian eggs (Crouch and Paton 2000), and we conducted larval and metamorph dipnet and visual encounter surveys (Thoms et al. 1997). We estimated the abundance of larvae and metamorphs (including juveniles) by species in the following classes: (1) 1–10, (2) 11–99, and (3) $\geq$100 individuals. Amphibian search effort was standardized to $\sim$20 minutes per visit. The numbers of visits made to assess amphibian populations among treatments were nearly equal (natural, median visits = 8.5, total visits = 88; agricultural, 9.5, 95; grazed, 8, 82; nongrazed, 9, 89) and were distributed over the breeding season from April to August. Some variation in numbers of visits was unavoidable because some ponds dried and filled, depending upon weather conditions.

Species richness was the total number of species observed at each pond over the breeding season, based on all observations of eggs, larvae, metamorphs, and juveniles, ranked in the following classes: (1) 1–2, (2) 2–3, (3) 4–5, and (4) 6 or more species. We developed an index of reproductive success for each species and for multiple species based on observations of eggs, larvae, metamorphs, and juveniles. This index integrates observations of multiple life stages over time into a single index value. It is a sensitive index, in that it separates ponds where large numbers of larvae and metamorphs were observed multiple times from ponds where few larvae and metamorphs were rarely observed. For example, we observed larvae at some grazed ponds prior to landowners turning the livestock into paddocks that contained the ponds. After the livestock had access to the ponds, the larvae were no longer observed and little or no successful reproduction occurred. For each species, reproductive success was ranked: high at ponds where the abundance class of larvae or metamorphs was $\geq$2 on at least three visits, medium at ponds where the abundance class of larvae, metamorphs, or juveniles was $\geq$2 on two or fewer visits or the abundance class of larvae, metamorphs, or juveniles was = 1 on at least three visits or egg masses were detected, and low at ponds not meeting the previous criteria. We also assigned each pond a ranking for multispecies reproductive success: ''overall high'' included ponds with two or more species with high reproductive success; all other ponds were ranked as ''overall low.'' Multispecies rankings are important to land managers who are unlikely to manage habitats for single species unless they are threatened or endangered. Calling data were not used in species richness estimates or indices of reproductive success; we observed amphibian species calling at a number of sites where we never observed any evidence of reproductive success (larvae or metamorphs) for that species.

Amphibian voucher specimens were collected to aid accurate identification of specimens and as a permanent public record. Voucher specimens were collected under Special Permit No. 9516 from the Minnesota Department of Natural Resources and deposited at the Bell Museum of Natural History, Minneapolis, Minnesota. We initially examined eggs and larvae under a dissecting microscope to verify field identifications; subsequent identifications were made in the field (Altig et al. 1998, Parmelee et al. 2002). Common names of species follow Crother (2001).

Habitat variables

We measured five sets of related a priori habitat predictors, including 26 variables representing aspects of the landscape surrounding the pond, pond morphometry, pond vegetation, aquatic predators, and water quality (Table 1). We made 1644 total visits to ponds in 2000 (842 visits) and 2001 (802 visits). We used International Coalition Land Use Land Cover maps (1990, 1:24 000 scale, see footnote 5) and NWI maps to measure landscape variables, including the total area of patches of forests, grasslands, and wetlands, and nearest neighbor distances to wetlands and forests within 500, 1000, and 2500 m of the breeding pond (Table 1). This range of distances corresponds to home range and movement distances for many amphibian species (Stebbins and Cohen 1995, Baker and Halliday 1999); other landscape studies of amphibian habitat have used this range of distances (Vos and Stumpel 1995, Knutson et al. 1999, 2000, Lehtinen et al. 1999).

Pond morphometry variables included pond area and maximum water depth. We measured the area of each pond from the digital land use land cover maps (Table 1) and we measured the maximum water depth in each pond to the nearest 0.1 m at each visit. We measured pond vegetation using a modification of aquatic plant sampling developed by Yin et al. (2000). We collected six samples (1.5 $\times$ 0.36 m) with a modified garden rake, spaced evenly around the perimeter (littoral zone) of each pond. The sum of index values for submergent, emergent, and floating-leaved vegetation, as well as algae represented a measure of total vegetation in the pond. We summed the index values for the percent cover of shoreline trees and shrubs as a measure of shoreline woody vegetation (Table 1).

We assessed the presence of aquatic predators on amphibian eggs and larvae at each pond in 2000 and 2001 (Table 1). We identified the presence of fish using visual encounter and dipnet surveys at each pond visit, in conjunction with the amphibian surveys. Fish were also surveyed using funnel traps (Peterka 1989). Potential macroinvertebrate predators on amphibian larvae were sampled at two locations in the littoral zone of each pond with three sweeps of a long-handled benthos net. We collected the two samples in contrasting vegetation types, if vegetation varied around the perimeter of the pond. We targeted riparian vegetation and shallow open sediments for sampling, habitats known to harbor most predatory macroinvertebrate species (Thorpe and Covich 1991). We sampled each pond three times (twice in June and once in July) in each year to determine the presence of potential invertebrate and fish predators; we did not attempt to estimate abundances for fish. We selected backswimmers, dragonfly nymphs, and water beetles as representative of potential invertebrate predators commonly found in the ponds. We included tiger salamander larvae as amphibian larval predators (Morin 1983).

We collected water quality samples at each pond from late April to late July in each year (2000, 193 samples; 2001, 156 samples; Table 1). Each composite pond sample was composed of separate water samples collected from four equidistant locations along the pond perimeter. Water samples were collected ~1 m from the shoreline at mid-depth. All water samples were labeled and immediately placed in coolers on ice and then refrigerated. Nutrient analyses were conducted within 30 days of collection at the Upper Midwest Environmental Sciences Center (UMESC) Water Quality Laboratory (La Crosse, Wisconsin, USA). Unfiltered water samples from both 2000 and 2001 were analyzed for total nitrogen and total phosphorus following standard methods after digestion (persulfate method; APHA 1998). Nutrient analyses were completed on a Bran+Luebbe TrAAcs 800 continuous flow analysis system (Bran and Luebbe, Delavan, Wisconsin, USA). Quality assurance for nutrient analyses included blind testing, sample splits, spike recovery, and routine evaluation of external standards. At each study site we also measured conductivity and turbidity in the field with calibrated water quality probes (e.g., YSI Model 57 multiparameter probe [YSI, Yellow Springs, Ohio, USA], Hach Model 2100P turbidimeter [Hach, Loveland, Colorado, USA]) according to standard methods (APHA 1998) and UMESC standard operating procedures.

Statistical analysis

We developed our statistical models using 2000 data and evaluated them using 2001 data. We formulated a priori hypotheses about expected relationships between amphibian reproductive success and habitat variables based on published literature and professional experience (Table 1). We expected that natural ponds would have the highest species richness and reproductive success, followed in rank order by nongrazed, grazed, and agricultural ponds. We expected that reproductive success would be higher where wetlands occupied more of the surrounding landscape, and vegetation cover in the pond was higher (Knutson et al. 1999, 2000, Mazerolle and Villard 1999). We expected that reproductive success would be lower where the abundance of predatory invertebrates, total nitrogen, and turbidity of the water were higher and fish were present (Skelly and Werner 1990, Hecnar and M'Closkey 1997, Rouse et al. 1999, Babbitt and Tanner 2000, Van Buskirk 2001). We expected that reproductive success for grassland-associated amphibians would be higher where the proportion of the landscape in grassland was higher and a similar relationship was expected between forests and forest-associated amphibians (Vogt 1981, Oldfield and Moriarty 1994, Harding 1997, Knutson et al. 1999, 2000). In addition, associations with species-specific life history traits such as requiring permanent vs. temporary water were expected (Knutson et al. 1999). Descriptive statistics were calculated for the predictor variables by adjacent land use. Hypothesis tests were used to detect any significant differences for each predictor variable among the treatments.

Because our response variables were categorical, with either two or three levels of reproductive success and four levels of species richness, our candidate sets of appropriate models were derived from the families of binary and ordinal logistic regression models, respectively. We first assessed whether our response variables were associated with the design components of our study. Using field data from 2000 and 2001, each response variable was tested for a year × treatment interaction effect and, if not significant, year and treatment main effects. Because of potential correlations within blocks, an adjustment for block effects was obtained and the models were fitted using generalized estimating equations (GEE) with pairwise comparisons among treatment categories based on empirical standard error estimates (Allison 2000). The method of GEE is an extension of general linear models that accounts for correlation within groups. All analyses were performed in SAS (SAS Institute 1999–2001). The effect of blocks on the standard errors of the treatments was found to be negligible, so block was not included in further model building.

We obtained habitat models by fitting all possible subsets of up to four predictor variables from the set of variables selected for each species. We included 20–23 variables in each analysis, depending upon species and based on our literature review (Table 1). We set the maximum number of predictors at four in a liberal effort to lower the admittedly large probability of Type I errors. This approach was taken because of the exploratory nature of our study and because the existing amphibian habitat literature supports only general a priori population-habitat hypotheses for each species. One purpose of the study was to reduce a fairly large set of landscape and pond habitat predictors to a smaller

TABLE 1. Habitat predictor variables selected a priori, based on the literature, with associated response variables (species richness and reproductive success) for agricultural ponds in Houston and Winona counties, Minnesota, 2000–2001.

Predictor variables, by group	Description	Response variables: Species	Response variables: Sources
Design			
TRTMT	one of four types of adjacent land uses: row crop agriculture; grazed grassland; nongrazed grassland; a natural wetland	all species	Bonin et al. (1997*a*, *b*), Bishop et al. (1999), Sparling et al. (2000), Bull et al. (2001), Joly et al. (2001)
Landscape			
FOREST500 FOREST1000 FOREST2500	total area (ha) of forests within 500, 1000, and 2500 m of pond center	spring peeper, gray treefrog, American toad	Oldfield and Moriarty (1994), Knutson et al. (1999, 2000), Mazerolle and Villard (1999), Guerry and Hunter (2002)
GRASSLAND500 GRASSLAND1000 GRASSLAND2500	total area (ha) of grassland within 500, 1000, and 2500 m	tiger salamander, chorus frog, leopard/pickerel frog	Oldfield and Moriarty (1994), Knutson et al. (1999, 2000), Guerry and Hunter (2002)
WET_AREA500 WET_AREA1000 WET_AREA2500	total area (ha) of permanent and temporary wetlands within 500, 1000, and 2500 m	all species	Oldfield and Moriarty (1994), Vos and Chardon (1998), Knutson et al. (1999, 2000), Lehtinen et al. (1999), Marsh et al. (1999), Skelly (2001)
NEAR_WET	distance (m) to next nearest wetland (all types)	all species	Lehtinen et al. (1999), Marsh et al. (1999), Skelly (2001)
NEAR_FOREST	distance (m) to next nearest forest	all species	Oldfield and Moriarty (1994), Knutson et al. (1999, 2000), Mazerolle and Villard (1999), Guerry and Hunter (2002)
Pond morphometry			
W_DEPTH_MEAN	pond depth (0.1 m)	all species	Pearman (1995), Babbitt and Tanner (2000), Paton and Crouch (2002)
POND_AREA	pond area (ha; permanent water directly associated with study site)	all species	Pearman (1995), Vos and Chardon (1998), Babbitt and Tanner (2000)
Pond vegetation			
TREESHRB	index of percentage of shoreline composed of trees or shrubs	all species	Skelly et al. (1999, 2002), Werner and Glennemeier (1999)
EMER	index of percentage of shoreline composed of emergent vegetation	all species	Knutson et al. (1999, 2000), Hazell et al. (2001)
VEG_SUM	sum of index values for emergent, submergent, floating-leaved, and algal vegetation in pond	all species	Knutson et al. (1999, 2000), Hazell et al. (2001)
Predator community			
FISH	presence or absence of fish in pond	all species	Kats et al. (1988), Hecnar and M'Closkey (1997), Hero et al. (1998), Adams (2000), Pilliod and Peterson (2001)
BCKSMR	sum of abundance indices for invertebrates: backswimmer (Hemiptera)	all species	Hero et al. (1998), Van Buskirk (2001)
DRGFLY	sum of abundance indices for invertebrates: dragonfly nymph (Odonata)	all species	Skelly and Werner (1990), McCollum and Leimberger (1997), Van Buskirk et al. (1997), Hero et al. (1998), Van Buskirk (2001)
WATBEE	sum of abundance indices for invertebrates: crawling water beetle (Coleoptera)	all species	Pearman (1995), Hero et al. (1998), Van Buskirk (2001)

TABLE 1. Continued.

Predictor variables, by group	Description	Response variables: Species	Sources
AMTRIN	maximum abundance index for tiger salamander larvae	all species except tiger salamander	Morin (1983), Kiesecker (1996), Lehtinen et al. (1999)
Water quality			
TOTNITR	mean total nitrogen (mg/L)	all species	Bishop et al. (1999), Rouse et al. (1999)
TURB	mean turbidity (NTU, nephelometric turbidity units)	all species	Hecnar and M'Closkey (1996), Bishop et al. (1999), Rouse et al. (1999)
COND	mean conductivity, siemens (μS/cm)	all species	Hecnar and M'Closkey (1996)
TOTPHOS	mean total phosphorus (mg/L)	all species	Bishop et al. (1999), Rouse et al. (1999)

set: those most likely to be associated with species richness and reproductive success.

To find the best approximating models, the set of candidate models were fit using the data from the 2000 field season and ranked according to Akaike's information criterion, as modified for small sample sizes (AIC_c; Akaike 1973, Burnham and Anderson 1998). Smaller AIC_c values are considered indicative of models that contain more information about response metrics. Furthermore, let $\Delta AIC_c = AIC_c - \min(AIC_c)$. Because a ΔAIC_c of four represents a candidate minimum cutoff value for an approximate 95% confidence set of the top models (Burnham and Anderson 1998), we used models with $\Delta AIC_c < 4$ to construct model and parameter weights. For each response metric, we obtained the five models with the smallest ΔAIC_c.

To obtain a final model, we retained the highest weighted predictors for which the 90% model-averaged confidence interval for the odds ratio excluded zero, with the constraint of a maximum of four predictors per model. We evaluated our final models for each species with 2001 data using Somer's *D*, percentage concordant, and R^2_{max} statistics as criteria for each model's predictive ability (Somers 1980, Guisan and Harrell 2000, Mitchell et al. 2001).

RESULTS

We identified 10 species of amphibians in the study ponds, including the tiger salamander (*Ambystoma tigrinum*), American toad (*Bufo americanus*), gray treefrog (*Hyla versicolor*), western chorus frog (*Pseudacris triseriata*), spring peeper (*Pseudacris crucifer*), green frog (*Rana clamitans*), wood frog (*Rana sylvatica*), northern leopard frog (*Rana pipiens*), and pickerel frog (*Rana palustris*) (Appendix A). Larval blue-spotted salamanders (*Ambystoma laterale*) were identified at a single natural wetland. Northern leopard frog and pickerel frog larvae could not be reliably differentiated in the field, so these species are considered together in the analysis. We excluded the wood frog and blue-spotted salamander from the statistical analysis because these species were rarely observed.

Fish species commonly collected included the brook stickleback (*Culea inconstans*), creek chub (*Semotilus atromaculatus*), green sunfish (*Lepomis cyanellus*), and central mud minnow (*Umbra limi*). Eight out of 10 natural ponds contained fish, while only three nongrazed, one grazed, and no agricultural ponds out of 10 ponds contained fish (Appendix B). Sunfish were only found in the grazed and nongrazed ponds, while sticklebacks, creek chubs, and mud minnows were found only in the natural and nongrazed ponds.

Weather patterns during the amphibian breeding season in 2000 and 2001 were contrasting. The spring of 2000 was relatively dry, followed by frequent rains beginning the end of May and continuing through July (NOAA 2000). In 2001, the spring was unusually cool and wet, followed by dry weather from June to August (NOAA 2001).

Natural ponds were characterized by a larger area of wetlands within 500 m, a shorter distance to the next nearest wetland, shallower mean pond depth, a higher proportion of trees and shrubs occupying the perimeter of the pond (along with nongrazed and agricultural ponds), and a higher probability of hosting fish compared with other pond types (Appendix B). Our natural ponds were heavily vegetated, while the grazed ponds had little aquatic or emergent vegetation, due to frequent disturbance. Agricultural and nongrazed ponds were intermediate in aquatic vegetative cover. Grazed ponds had higher total phosphorus concentrations and turbidity compared with natural ponds (Appendix B). We observed a trend for nitrogen to be higher in grazed and agricultural ponds and lower in nongrazed and natural ponds.

Community responses

There were no significant year × treatment interaction effects and there were no significant year or treatment effects for species richness or for overall re-

TABLE 2. Habitat predictors and odds ratios (model-averaged) for agricultural ponds in Houston and Winona counties, Minnesota, 2000–2001.

Predictors, by species	Odds ratio†	90% CI for odds ratio
Species richness		
POND_AREA	0.12	(0.03, 0.55)
FISH	0.08	(0.01, 0.43)
AMTRIN	6.61	(1.81, 24.1)
TOTNITR	0.04	(0.01, 0.33)
Multispecies reproduction		
FISH	3.6×10^{-4}	(4.4×10^{-7}, 0.29)
VEG_SUM	0.23	(0.06, 0.88)
TOTNITR	5.1×10^{-11}	(2.6×10^{-20}, 0.10)
American toad		
WET_AREA500	0.67	(0.48, 0.94)
W_DEPTH_MEAN	0.81	(0.71, 0.93)
BCKSMR	2.48	(1.40, 4.36)
TURB	0.94	(0.91, 0.98)
Chorus frog		
GRASSLAND2500	1.01	(1.001, 1.02)
W_DEPTH_MEAN	0.89	(0.79, 0.996)
TREESHRB	1.45	(1.003, 2.09)
COND	0.99	(0.98, 0.999)
Gray treefrog		
FOREST1000	1.03	(1.004, 1.05)
BCKSMR	2.15	(1.22, 3.78)
COND	0.98	(0.97, 0.99)
TOTNITR	0.01	(3.0×10^{-4}, 0.28)
Green frog		
TREESHRB	0.80	(0.73, 0.88)
WATBEE	0.57	(0.49, 0.67)
TURB	0.95	(0.94, 0.97)
TOTNITR	0.08	(0.05, 0.14)
Leopard and pickerel		
TRTMT: AGRIC VS. NATUR	0.38	(0.11, 1.40)
TRTMT: GRAZE VS. NATUR	0.12	(0.02, 0.64)
TRTMT: NGRAZ VS. NATUR	0.13	(0.03, 0.53)
NEAR_FOREST	1.01	(1.00, 1.02)
GRASSLAND1000	1.05	(1.01, 1.09)
WATBEE	2.12	(1.21, 3.73)
Spring peeper		
NEAR_WET	0.99	(0.989, 0.998)
NEAR_FOREST	0.98	(0.966, 0.996)
FOREST2500	1.01	(1.001, 1.012)
TURB	0.93	(0.87, 0.98)
Tiger salamander		
NULL		

† The odds ratio is interpreted as in this example: The odds of being in a higher category of species richness are 6.61 times higher for each unit increase in tiger salamander abundance (AMTRIN). Odds ratios <1 correspond to negative relationships.

productive success (Appendix C). In the model selection analysis, landscape variables did not appear in the final model-averaged model for either species richness or multispecies reproductive success (Table 2, Appendix D). The final models for species richness and multispecies reproductive success are composed of factors associated with the pond itself, including the predator community, vegetation, and water quality. The final model for species richness includes pond area, fish, the abundance of tiger salamander larvae, and total nitrogen (Table 2, Fig. 2). The final model for multispecies reproduction includes total nitrogen, fish, and emergent vegetation cover (Table 2, Fig. 3).

Single species responses

When we examined treatment and year effects, there were no significant year × treatment interaction effects for any species. We found treatment effects for the gray treefrog ($P = 0.0081$) and the spring peeper ($P = 0.0257$). Gray treefrog reproductive success was higher in nongrazed and agricultural ponds than in natural ponds and grazed ponds (Appendix C). Spring peeper

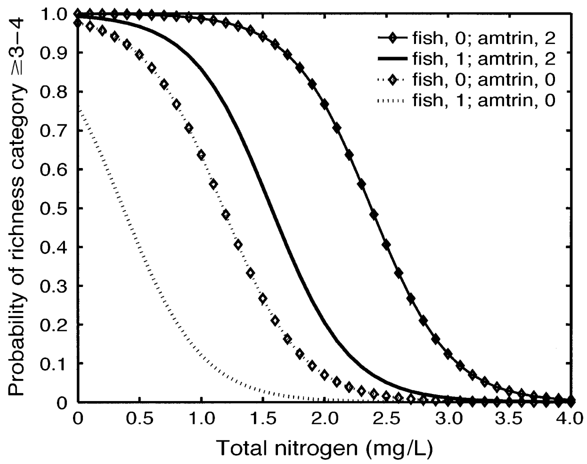

FIG. 2. Effects of total nitrogen, adjusted for tiger salamander (''amtrin'') abundance and fish presence (''fish''), on the probability of amphibian species richness of 3 or higher in agricultural ponds in Houston and Winona Counties, Minnesota, 2000. The probability of high species richness, based on the logistic regression model, was estimated by: prob = $1/[1 + \exp(-a_i + 2.13 \times \mathrm{POND\_AREA} + 2.55 \times \mathrm{FISH} - 1.89 \times \mathrm{AMTRIN} + 3.15 \times \mathrm{TOTNITR})]$, where a_i is 1.43, 4.14, and 12.93 for the probability of being in species richness category 6 or more, 3–4 or higher, and 2–3 or higher, respectively. (See Table 1 for key to variables in regression model.)

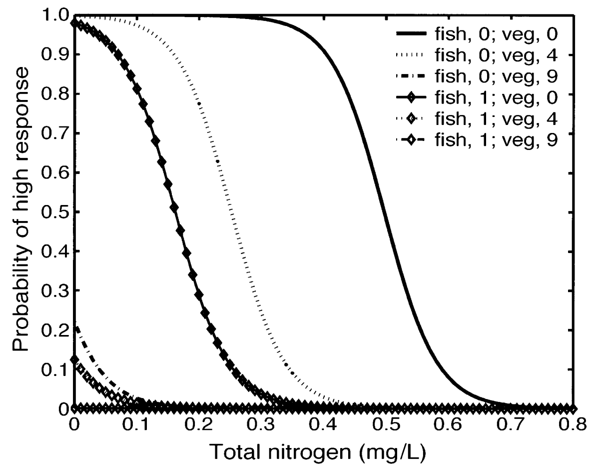

FIG. 3. Effects of total nitrogen, adjusted for vegetation (''veg'') and fish presence (''fish''), on the probability of high reproductive success for two or more amphibian species in agricultural ponds in Houston and Winona Counties, Minnesota, 2000. The probability of high reproductive success for all species combined, based on the logistic regression model, was estimated by: prob = $1/[1 + \exp(-11.78 + 1.45 \times \mathrm{VEG\_SUM} + 7.94 \times \mathrm{FISH} + 23.70 \times \mathrm{TOTNITR})]$. (See Table 1 for key to variables in regression model.)

reproductive success was higher in nongrazed and agricultural ponds than in grazed ponds. In the model selection analysis, treatment also appeared in the model-averaged (final) model for the leopard/pickerel frog; natural ponds supported more reproductive success than the other pond types (Table 2, Appendix C). We found no significant differences among treatments for reproductive success of the American toad, western chorus frog, or green frog. The western chorus frog reproductive success model contained a significant main effect for year ($P = 0.0184$); 15 ponds were in the high reproductive success category in 2000, while only five were so classed in 2001 (Appendix C).

Landscape variables were represented in all of the model-averaged individual species models except for the green frog (Table 2, Appendix D). Different species were associated with different landscape metrics. Exploratory analysis revealed that landscape metrics measured from increasing distances around the ponds (e.g., 500, 1000, 2500 m radii) were highly correlated with one another.

Among the variables associated with the pond itself, water quality variables appear in all the single-species models except the northern leopard/pickerel frog, where water quality variables may have been replaced by a treatment effect (Table 2). Predators appear in four single species models, pond vegetation in two models, and pond morphometry in one.

Validation

Final models derived from the year 2000 data showed predictive ability with the 2001 data ($D > 0.20$, Mitchell et al. 2001), except for the American toad model ($D = 0.17$). The explanatory power of the models for 2001 was generally lower compared with 2000 (Table 3). The models for species richness and multispecies reproductive success were 73–75% concordant between predicted probabilities and observed responses for data collected in 2001. Our models explained moderate proportions (29–83%) of the variability in the data sets in 2000 and lower proportions (7–46%) of the variability in 2001 (Table 3).

DISCUSSION

Agriculture adjacent to breeding ponds

To our knowledge, our study is the first to report potentially negative effects on amphibian reproduction associated with grazing and direct livestock access to ponds. Our observations of low multispecies reproductive success and a trend toward low species richness in grazed ponds, as well as low reproductive success for the spring peeper, leopard/pickerel frog, and gray treefrog can be attributed to poor water quality and disturbance. Grazed ponds experience disturbance from livestock wading and defecating in the pond. This activity uproots aquatic and emergent vegetation in the pond and prevents trees and shrubs from taking root along the perimeter of the pond. The direct input of high levels of nitrogen (urine and manure) and the turbidity induced by livestock disturbance leads to poor water quality, low oxygen concentrations, and a generally adverse environment for amphibian eggs and tadpoles. Highly productive ponds experience wide swings in dissolved oxygen and pH that can be detri-

TABLE 3. Validation of the best habitat models for agricultural ponds in Houston and Winona counties, Minnesota, 2000–2001.

Species	Model predictors	2000 Somer's *D*	2000 Concordance (%)	2000 R^2	2001 Somer's *D*	2001 Concordance (%)	2001 R^2
Species richness (8†)	POND_AREA(−), FISH(−), AMTRIN(+), TOTNITR(−)	0.75	87.0	0.72	0.46	72.6	0.28
Multispecies reproduction (25)	VEG_SUM(−), FISH(−), TOTNITR(−)	0.95	97.4	0.83	0.94	74.6	0.26
American toad (7)	W_DEPTH_MEAN(−), WET_AREA500(−), BCKSMR(+), TURB(−)	0.75	87.4	0.58	0.17	58.1	0.07
Chorus frog (33)	COND(−), GRASSLAND2500(+), W_DEPTH_MEAN(−), TREESHRB(+)	0.66	83.2	0.39	0.62	81.2	0.23
Gray treefrog (29)	COND(−), TOTNITR(−), FOREST1000(+), BCKSMR(+)	0.89	93.9	0.77	0.60	80.0	0.38
Green frog (179)	TURB(−), TREESHRB(−), TOTNITR(−), WATBEE(−)	0.51	75.0	0.32	0.67	83.7	0.46
Leopard and pickerel (19)	NEAR_FOREST(+), TRTMT(AG−, GR−, NG−), WATBEE(+), GRASSLAND1000(+)	0.51	75.1	0.32	0.42	70.4	0.19
Spring peeper (22)	TURB(−), NEAR_FOREST(−), NEAR_WET(−), FOREST2500(+)	0.54	76.9	0.29	0.41	70.6	0.20
Tiger salamander‡ (56)	WET_AREA500(−), POND_AREA(+), TREESHRB(−), WATBEE(+)	0.85	92.6	0.66	0.66	82.7	0.41

Note: Somer's *D* is a measure of association that varies between 0 and I, with larger values corresponding to stronger associations.

† The number of models with $\Delta AIC_c < 4$, which were used to compute the Akaike weights.

‡ Model-averaged model was null; $\Delta AIC_c = 0$ model is used for validation.

mental to the survival of amphibian eggs and larvae (Freda and Gonzalez 1986). If nitrate concentrations are high enough, adverse sublethal effects or even mortality may result (Baker and Waights 1994, Hecnar 1995).

Livestock grazing and loafing in water bodies are widely recognized as creating negative geomorphological (Trimble 1994) and water quality (Waters 1995) conditions. In a study of livestock grazing intensity in Australian wetlands, frog communities, species richness, and some individual species of frogs declined with increased grazing intensity (Jansen and Healey 2003). In contrast, Bull et al. (2001) did not find differences in the relative abundance of larvae of Pacific treefrogs (*Pseudacris regilla*) or long-toed salamanders (*Ambystoma macrodactylum*) between fenced and unfenced stock ponds in Oregon. However, fencing streambanks to exclude livestock failed to produce an immediate increase in amphibian species richness or abundance (Homyack and Giuliano 2002).

Agronomic research indicates that allowing livestock unrestricted access to ponds may also have adverse effects on agricultural production. Willms et al. (2002) found that yearling heifers and calves with cows drinking clean water gained more mass than those drinking pond water contaminated with manure. Cows drinking clean water also spent more time grazing and less time resting than those drinking contaminated water. We conclude that restricting direct livestock access to farm ponds by fencing will improve habitat quality for amphibians and provide a more healthful environment for livestock. The pond can continue to serve as a water source for livestock by employing a pump to deliver pond water to a trough (Godwin and Miner 1996).

Ponds adjacent to both grazed land and row crop agriculture tended to have more turbidity and elevated concentrations of nitrogen and phosphorus compared with natural ponds and those adjacent to nongrazed land (Appendix B), and these factors appear frequently in our models (Table 2). The negative effects of nitrogen on anurans observed in this study were not unprecedented (Bishop et al. 1999); however, we observed these negative effects at relatively low total nitrogen concentrations (0.1 to 14 mg/L, Appendix B, Figs. 2 and 3). Data summarized by Rouse et al. (1999) show lethal effects of nitrate for a variety of anurans ranged from 14 to 385 mg/L, while sublethal developmental effects on larvae ranged from 2.5 to 10 mg/L nitrate. These responses were species and life-stage specific, with early life stages being more sensitive than adults, and bufonid adults tending to be the least sensitive species and life stage. Our findings are consistent with research by Bishop et al. (1999) documenting reduced amphibian diversity and abundance in Ontario. They found that water from agriculturally impacted zones contained relatively high phosphorus (reactive phosphorus, 0.8 mg/L), nitrogen (total Kjeldahl nitrogen, 4.2 mg/L), and ammonia (total ammonia nitrogen, 0.2 mg/L). Despite the uncertainty of causal mechanisms in the field, it is clear from many other studies that nitrogenous compounds have potent negative effects on amphibian development, growth, and survival (Huey and Beitinger 1980*a*, *b*, Baker and Waights 1994, Marco and Blaustein 1999).

Even though agricultural chemicals are responsible for adverse effects on amphibians (Bonin et al. 1997*a*, Hecnar 1997, Sparling et al. 2000, Davidson et al. 2002), their effects vary depending upon concentrations and other factors. We detected low concentrations of atrazine ($<$0.1–0.5 μg/L) and di-ethyl atrazine ($<$0.1–0.3 μg/L), as well as trace amounts ($<$0.1 μg/L) of metolachlor, alachlor, and acetochlor in a subset of our natural and agricultural study ponds (J. Elder, *unpublished data*). These concentrations were lower than concentrations documented in the laboratory to have negative effects on amphibian morbidity and mortality (Howe et al. 1998, Larson et al. 1998, Allran and Karasov 2000, 2001). Recent research links low levels of atrazine with sublethal effects that may be depressing amphibian populations generally (Hayes et al. 2002). However, breeding pond adjacency to row crop agriculture, by itself, had little measurable effect on amphibian species richness or reproductive success in our study.

Characteristics of the pond vs. the landscape

We found support for the hypothesis that pond factors are more important than landscape variables to amphibian community responses (species richness and reproductive success). One of the most important pond-level factors was the presence of fish. Because of the high risk of predation by fish, most amphibians require fishless habitats to breed and survive (Lannoo 1998). Historically, small wetlands and prairie potholes have provided such habitats, remaining fishless due to drought-induced drying and hypoxia with resultant summer- and winterkills. Small ponds are less likely to have fish and perhaps other invertebrate predators than large ponds (Pearman 1995). Our finding that species richness was negatively associated with pond area concurs with the idea that many amphibian populations depend upon temporary water bodies (Skelly 1996, Snodgrass et al. 2000). Our species richness and multispecies reproductive models showing negative associations with fish are in accord with most published literature on fish/amphibian interactions (Kiesecker and Blaustein 1998, Adams 2000). Biogeographic patterns of salamander and frog distributions in the eastern United States have been correlated to the susceptibility of the amphibians to fish predators and the distribution of these predators (Petranka 1983, Kats et al. 1988). In the eastern United States, several taxa of amphibians do co-occur with fish (e.g., *Rana catesbeiana*, *Rana clamitans*, *Bufo americanus*, and *Notophthalmus viridescens*); these species contain either unpalatable eggs or larvae (Kats et al. 1988). Our results compare with Hecnar and M'Closkey (1998), who found anuran species richness to be more strongly related to the presence of predatory fish than to water chemistry. In contrast, Lehtinen et al. (1999) observed higher amphibian species richness in wetlands with fish. However, both our data and those of Lehtinen et al. (1999) support the idea that the tiger salamander, another amphibian predator (Skelly 1997), is associated with higher species richness. Tiger salamanders may indirectly affect the growth and survival of other amphibian larvae and therefore positively influence community species richness, similar to the demonstrated role of *Notophthalmus viridescens* (Fauth 1990, Morin 1995, Kurzava and Morin 1998).

We expected that more aquatic (submergent and emergent) vegetation in the pond would be positive for amphibian reproduction (Laurila 1998), providing more attachment sites for eggs and refuges from predators, but our data indicate the opposite was true. Aquatic vegetation variables appearing in the models were always negative. We reasoned that perhaps our natural ponds were more likely to have both fish and abundant vegetation and that the vegetation relationships were confounded by the presence of fish. Examination of the data shows that natural ponds were more likely to have fish, but exploratory analyses controlling for fish presence still resulted in vegetation variables with a negative relationship with reproductive success. Another possibility is that abundant vegetation causes observer detection problems, reducing the apparent abundance of larvae and metamorphs; we cannot rule this out as an explanation. However, natural history information indicates that several species may prefer breeding sites with moderate or low amounts of vegetation rather than heavily vegetated sites (Vogt 1981).

The failure of landscape variables to appear in our species richness and multispecies reproductive success models can be attributed to contrasting landscape associations for different species. For example, our model for the spring peeper supports the hypothesis that reproductive success should be higher where other ponds or wetlands are nearby (Vos and Stumpel 1995, Findlay and Houlahan 1997, Knutson et al. 1999, Lehtinen et al. 1999). Little information is available regarding dispersal distances for the spring peeper, but our results may reflect a smaller home range or restricted dispersal distance for this small-bodied anuran. In contrast, for the American toad, a larger, more generalist species, reproductive success was associated with less area of wetlands within 500 m of the breeding pond, possibly reflecting a tolerance of drier habitat conditions. When individual species have contrasting responses to habitat factors, the influence of these factors may be masked when multiple species are considered together. This allows pond-level factors, such as fish or water quality to emerge. Hazell et al. (2001), working in Australia, also found that different landscape factors were important to individual species but not the overall amphibian community. This has implications for management, as habitat features important to an individual species of management concern may contrast with habitat associations observed for the amphibian community in general. However, some studies have identified landscape associations at the community level. Lehtinen et al. (1999) found that landscape factors from 500 to 2500 m away from the pond influenced species richness. Beebee (1985) found that landscape variables were more predictive of amphibian diversity than pond characteristics, including water chemistry. Hecnar and M'Closkey (1998) found anuran species richness to be more strongly related to the presence of surrounding landscape variables (forest cover) than to water chemistry. In their study, regional deforestation was believed to be an important factor affecting amphibian communities.

The relative influence of landscape vs. pond variables has important implications for modeling amphibian habitat quality at the regional scale. It is more difficult to develop regional maps of pond-specific habitat variables such as water quality, vegetation structure, pond morphometry, and the predator community, than it is to derive landscape metrics (e.g., area of forests, grasslands, or wetlands) from simple land cover maps. For example, if water quality information is needed to assess habitat suitability, spatial (GIS) models lacking this information will not be sufficient to identify high quality amphibian breeding sites. However, we are encouraged by our validation results, especially given the contrasting weather conditions in the two years. Even though climatic conditions can range from very wet to very dry in any given location, there may be hope for the development of generalized habitat models that perform reasonably well to predict amphibian habitat quality.

Single species associations

The models for the chorus frog and northern leopard/pickerel frog (grassland associates), gray treefrog and spring peeper (forest associates), and American toad (generalist) are concordant with their known habitat associations (Harding 1997, Knutson et al. 2000). Our data concur with a regional study of anuran calling data from Wisconsin and Iowa that described the general forest and grassland habitat associations identified above (Knutson et al. 2000). Our ability to detect relatively stable habitat relationships at spatial scales ranging from regional to local, using both calling data and indicators of reproductive success, indicates that these general habitat associations can now be used to make general forecasts about the effects of management actions. For example, provisions of the 2002 Farm Bill may be expected to influence specific grassland-associated amphibian populations if the overall amount of grassland in a region is projected to increase or decrease.

Our analysis also revealed habitat associations for individual species that are new or contrast with previous work. The American toad and chorus frog were both associated with shallow water. This compares with another study from the Midwest (Indiana, USA) where the chorus frog was most likely to occur at sites with intermediate permanency (Kolozsvary and Swihart 1999). We failed to find an expected association between green frogs and water depth (permanent water; Oldfield and Moriarty 1994). However, our natural wetlands tended to be relatively shallow, but retained some water even during dry periods (probably due to ground water input). Therefore, water depth was not a strong indicator of permanent water in our study. We were unable to confirm a grassland association for the tiger salamander (Harding 1997, Knutson et al. 2000). The tiger salamander model, based on AIC_c, included a negative association with trees and shrubs in the pond shoreline (Table 3), indicating that the tiger salamander may respond more to shoreline vegetation than to the surrounding landscape.

Pond design and management

Best management practices for increasing amphibian species richness in agricultural landscapes include providing small ponds, with low nitrogen concentrations, that support tiger salamander populations but no fish (Fig. 2). To achieve a 0.5 probability of observing three or more species, total nitrogen levels should be <0.05 mg/L when tiger salamanders are absent and fish are present, but when tiger salamanders are abundant and fish are absent, total nitrogen levels can range up to 2.5 mg/L.

Best management practices for improving overall amphibian reproductive success include providing ponds with low nitrogen concentrations, low amounts of vegetation, and no fish (Fig. 3). The presence of fish interacted synergistically with emergent vegetation and total nitrogen concentrations to reduce the probability of high reproductive success in ponds. When fish and vegetation were absent from a pond, the probability of two or more amphibian species exhibiting high reproductive success was significantly higher at a given nitrogen concentration than when fish were present. For example, amphibians in a pond with no fish or vegetation would have a 0.5 probability of attaining high reproductive success with total nitrogen concentrations of 0.45 mg/L (Fig. 3). With fish present, but no vegetation, the same reproductive success would occur at a total nitrogen concentration of 0.16 mg/L. With both fish and high density of vegetation, the model predicts that the probability of reproductive success would not reach 0.1, regardless of total nitrogen concentrations.

In some agricultural regions like the Driftless Area, natural wetlands are scarce and constructed agricultural ponds may represent important alternative breeding habitats for amphibians. Informed agricultural pond design and management can improve breeding habitat quality. The USDA has published engineering guidelines for building agricultural ponds (Deal et al. 1997), but ecological guidelines are also needed. Pond management guidelines that derive from our results include limiting livestock access to the pond, limiting nitrogen inputs, and avoiding the introduction of fish. If fish populations are already established and removing them is not an option, increasing habitat diversity may help provide refuges for amphibian breeding (Kats et al. 1988, Sih et al. 1988). Wide grassed buffer strips around the perimeter of the pond help reduce sediment, nutrient, and water flow into ponds during storm events (Castelle et al. 1994). Small, constructed farm ponds, properly managed, may help sustain amphibian populations in landscapes where natural wetland habitat is rare.

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APPENDIX A

A figure showing the amphibian species present in 40 ponds and four types of surrounding land uses in Houston and Winona Counties, Minnesota, 2000–2001 is available in ESA's Electronic Data Archive: *Ecological Archives* A014-010-A1.

APPENDIX B

A table of summary statistics for the top predictor variables for agricultural ponds in Houston and Winona Counties, Minnesota, 2000 is available in ESA's Electronic Data Archive: *Ecological Archives* A014-010-A2.

APPENDIX C

Figures showing overall amphibian reproductive success and species richness by year and land use in Houston and Winona Counties, Minnesota, 2000–2001 are available in ESA's Electronic Data Archive: *Ecological Archives* A014-010-A3.

APPENDIX D

A table of model-averaged predictor weights for predictor variables in agricultural ponds in Houston and Winona Counties, Minnesota, 2000–2001 is available in ESA's Electronic Data Archive: *Ecological Archives* A014-010-A4.

APPENDIX E

Color versions of the two photographs in Plate 1 (a natural wetland and an agricultural constructed pond in Winona County, Minnesota) are available in ESA's Electronic Data Archive: *Ecological Archives* A014-010-A5.