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Factors Influencing Anuran Wetland Occupancy in an Agricultural Landscape

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Abstract: Habitat disturbance is an important cause of global amphibian declines, with especially strong effects in areas of high agricultural use. Determining the influence of site characteristics on amphibian presence and success is vital to developing effective conservation strategies. We used occupancy analysis to estimate presence of four anuran species at wetlands in northern Iowa as a function of eight environmental covariates hypothesized to affect occupancy: fish and salamander abundance, invertebrate density, aquatic vegetative cover, wetland area, atrazine concentration in water, surrounding agricultural land use, and an overall wetland health score (wetland condition index [WCI]). We surveyed 27 wetlands multiple times in 2015 and 2016. Leopard Frogs (*Lithobates pipiens*) and American Toads (*Anaxyrus americanus*) were observed at 100% of the sites, Boreal Chorus Frogs (*Pseudacris maculata*) at 96%, and Gray Treefrogs (*Hyla* spp.) at 81%. Wetland site occupancy for all species in our study ranged from 0.23 (*Hyla* spp. tadpoles) to 0.95 (*L. pipiens* adults), indicating that agricultural wetlands can provide refuge or habitat for amphibians. Fish abundance, percentage of cropland cover within 500 m of the wetland, and salamander abundance were among the variables best supported by our models although their estimated effects were weak. Wetland area, atrazine concentration, vegetative cover, and WCI also influenced occupancy probability, but for only a small number of species and life stages. The direction of predicted effects varied by species and life stage. Despite only weak evidence that the environmental factors we measured influenced anuran occupancy, our results provide insights for managers seeking to understand how amphibians use landscapes modified by agriculture.

Key words: Amphibian; Frog; Habitat; Iowa; Modeling

Habitat disturbance is among the greatest threats to biodiversity worldwide (Vitousek 1992; Sala et al. 2000). One of the primary causes of disturbance is the conversion of natural landscapes to agriculture (Tscharntke et al. 2005; Turner et al. 2007). Currently, almost 40% of the earth's total land area is used for agricultural production (Bruinsma 2003). Wildlife management in modified habitats is important to preserve biodiversity (Frissell and Bayles 1996) but conservation in disturbed landscapes can be challenging without understanding landscape characteristics that influence populations. Loss of natural habitat has varying effects on organisms, but species with limited dispersal abilities such as amphibians might be disproportionately affected when habitat connectivity is reduced (Cushman 2006).

Despite sensitivity to environmental disturbance, amphibians occur in many landscapes modified for agricultural production. Some frogs indigenous to Japan rely on rice fields that have replaced natural wetlands and risk extinction without access to these modified habitats (Kato et al. 2010). In Europe, Natterjack Toads (*Epidalea* [*Bufo*] *calamita*) persist in cultivated areas using marginal habitat for refuge in the postbreeding season (Miaud and Sanuy 2005). As agriculture intensifies, amphibians will continue to use, or attempt to use, modified habitats. Stressors (e.g., contaminants, disease, and nonnative predators) increase the need for proactive management efforts to mitigate amphibian declines in agricultural landscapes (Kingsbury and Gibson 2012). Amphibians in these suboptimal habitats might be more vulnerable to threats and have an elevated need for protection or management.

For conservation strategies to be effective, it is vital to understand how, and how successfully, amphibians are using modified landscapes. Successful use of a habitat can be characterized by the presence of breeding adults and multiple age classes (indicating recruitment; Semlitsch 2001; Muths et al. 2014). Because amphibians use both aquatic and terrestrial habitats, their presence can be affected by a combination of site and landscape attributes (Kingsbury and Gibson 2012). Determining attributes that influence amphibian distribution and success in modified habitats is relevant to a wide range of amphibians living in such habitats worldwide.

In Iowa, amphibians persist despite the fact that more than 90% of the landscape has been converted from grasslands and wetlands to row-crop agriculture during the past two centuries (Bishop 1981; Bogue 1994; Gallant et al. 2011). Seventeen species of frogs and toads inhabit Iowa's agricultural landscape (IDNR 2006). Although amphibians are present in these modified habitats, amphibians in the Midwestern United States are estimated to be declining at a rate of >3% annually (Grant et al. 2016) and species once abundant, such as Northern Leopard Frogs (*Lithobates pipiens*), are less common (Hemesath 1998; Lannoo 1998). To understand the relationships among amphibian presence and environmental factors, we used occupancy modeling (MacKenzie et al. 2002) to explore which characteristics are associated with presence of multiple anuran species in Iowa wetlands.

Occupancy analysis facilitates the use of data with detection probabilities <1 to explore the influence of site-specific attributes (MacKenzie et al. 2002). We developed hypotheses about the effect of environmental covariates that are likely to affect the occupancy of anurans on this landscape: fish abundance, abundance of Tiger Salamanders

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Table 1.—Hypotheses of covariate effects on probability of amphibian occupancy and detection in Iowa. Fish and salamander abundance were measured as number of individuals (n) and aquatic invertebrate density was recorded as number of individuals/m^3. Aquatic vegetation cover was measured as percentage of open water cover, and cropland at 500 m was the percentage of land planted in agricultural crops (corn and soybeans) within a 500-m radius of the wetland edge.

Covariate	Hypothesized effect	Reasoning
Occupancy		
Fish abundance (n)	Negative	Amphibian predator, precludes use by amphibians (Hecnar and M'Closkey 1997; Hero et al. 1998; Herwig et al. 2013)
Salamander abundance (n)	Negative	Amphibian predator (Maret and Collins 1994)
Aquatic vegetation cover (%)	Positive	Vegetation provides cover and food source for tadpoles (Hartel et al. 2007)
Aquatic invertebrate density (n/m^3)	Positive	Provides food source for amphibians (Babbitt et al. 2003)
Wetland area (ha)	Positive	Species–area relationship: larger areas tend to contain more species (Connor and McCoy 1979; Findlay and Houlahan 1997)
Atrazine concentration (μg/L)	Negative	Atrazine might have indirect negative effects on amphibians by disrupting immunity or reproductive success (Mann et al. 2009; Rohr And McCoy 2010)
Cropland at 500 m (%)	Negative	Cropland alters amount of terrestrial habitat and limits dispersal, lowering occupancy, and might lead to dissection because of low soil moisture content relative to grassland (Tufekcioglu et al. 2001; Collins et al. 2009)
Wetland condition index (score 1–5)	Positive	Amphibians are associated with good wetland health (Dunson et al. 1992; Welsh and Ollivier 1998)
Detection		
Survey air temperature (°C)	Positive/Negative	Amphibians are less active at temperature extremes, making them more difficult to detect during surveys
Aquatic vegetation cover (%)	Negative	Reduces visibility and obstructs dip net sweeps

(*Ambystoma tigrinum*), aquatic vegetation cover, aquatic macroinvertebrate density, wetland area, dissolved atrazine concentration, and cropland cover within 500 m radius of the wetland (Table 1). We also investigated whether an overall wetland condition index (WCI), developed using our focal covariates plus other environmental characteristics, could predict anuran presence (Sundberg et al. 2016). We hypothesized that the probability of detection depends on time, and was influenced by survey-specific air temperatures and the amount of aquatic vegetation cover (Table 1).

Materials and Methods

Study Sites

We surveyed 27 permanent or semipermanent flooded palustrine wetlands (Fig. 1; Cowardin et al. 1979) in the Prairie Pothole region of north-central Iowa. Wetlands were selected by Sundberg et al. (2016) using previously collected biophysical data (e.g., fish presence and chloride concentration), site visits, and assessment of orthophotos to ensure broad variation in landscape and wetland characteristics across study sites. Wetlands were owned privately ($n = 4$), by

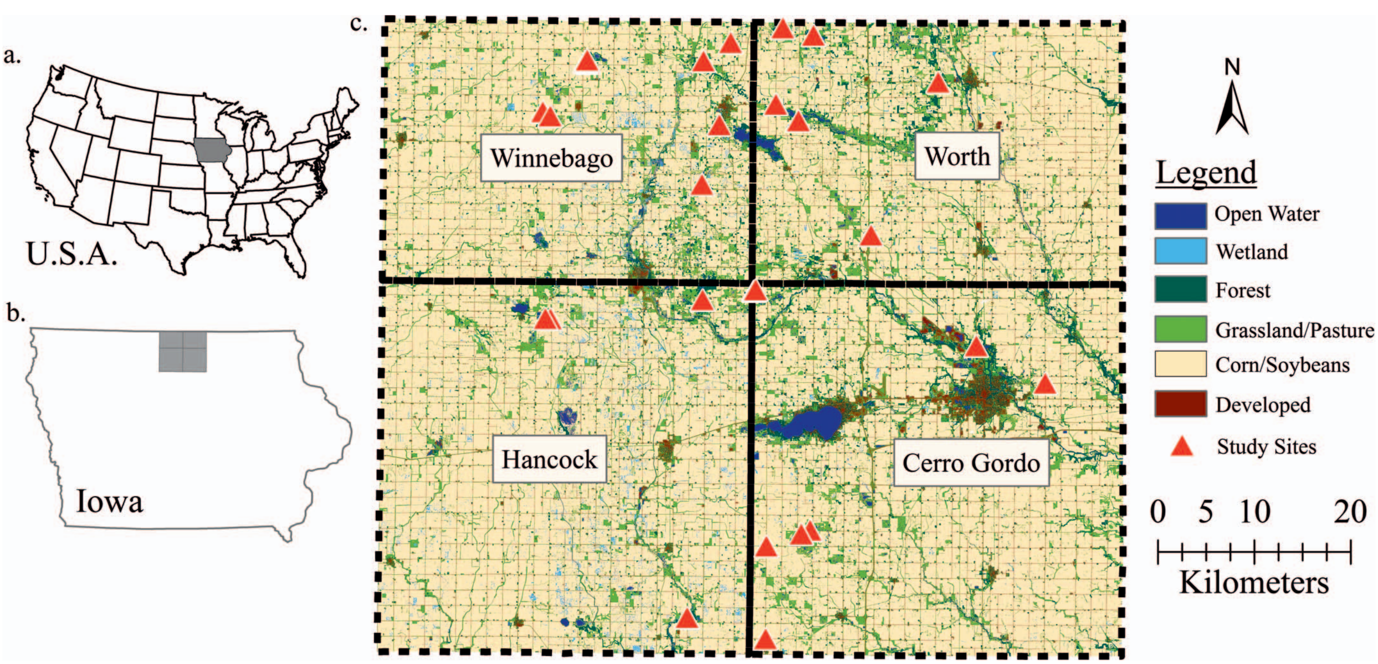

Fig. 1.—Site map: (a) depicts Iowa's location within the United States (indicated by gray shading), (b) depicts the location of counties where the study took place within Iowa (indicated by gray shading), and (c) depicts the locations of the 27 wetland study sites with land cover information. This map was created using ArcGIS (v.10.5.1; ESRI 2018).

county conservation boards ($n = 11$), or by the Iowa Department of Natural Resources (IDNR; $n = 12$; see Appendix S1 in the Supplemental Materials available online).

Study Species

We conducted surveys of four anuran species: American Toads (*Anaxyrus americanus*), Northern Leopard Frogs (*Lithobates pipiens*), Boreal Chorus Frogs (*Pseudacris maculata*), and Gray Treefrogs (Gray Treefrogs [*Hyla versicolor*] and Cope's Gray Treefrogs [*Hyla chrysocelis*] were treated as one taxon; IDNR 2006). None of these species are listed as threatened or endangered in Iowa although there are documented declines in population sizes of *L. pipiens*, *P. maculata*, and *Hyla* spp. (Lannoo et al. 1994; Knutson et al. 2000).

Amphibian Surveys

Surveys were conducted from May to August in 2015 and 2016. We used a combination of visual encounter, call, and dip-net surveys to determine the presence of each species in a wetland (Crump and Scott 1994; Thoms et al. 1997). Each wetland was surveyed four times in 2015 and three times in 2016 ($n = 7$ surveys). Surveys were conducted by one or two independent observers walking the perimeter of the wetland to visually detect adults and egg masses and listen for vocalization of adult males. Dip-net samples were taken every 3 m to sample tadpole and metamorph life stages. Surveys lasted 1–2 h, depending on the length of the wetland perimeter.

Environmental Data Collection

Environmental variables (Table 1) were collected in 2015 as part of another study (Sundberg et al. 2016). Fish and salamander presence and abundance (n) were measured once in each wetland using three fyke nets and three mini fyke nets spaced evenly and oriented perpendicular to the wetland edge for 24 h. We did not scale abundance of fish or salamanders by wetland size for analysis because of the variability of water volume at our sites (i.e., sites with similar areas but different depths could have different densities). Macroinvertebrates were sampled using a stovepipe sampler at five evenly spaced locations in open water around the wetland edge. Percentage of aquatic vegetation cover was estimated once in July by establishing five parallel transects at evenly spaced locations across each wetland, dividing each transect into five sections of equal length, and estimating plant cover from one randomly selected 1.0-m^2 plot located within each transect section. Percentage of plant cover was averaged across all 25 plots in the wetland. In June, water samples were collected and analyzed for atrazine (USEPA 2014). Preemergent herbicides are applied to the surrounding landscape once, typically in spring, and are flushed from the fields during late spring and early summer rains (Thurman et al. 1991). Because the study was designed to capture amphibian abundance, we likely missed the herbicide peak. Based on a previous study in Iowa, atrazine concentrations are still elevated during the month of June (Smalling et al. 2015). Wetland area and the percentage of crop cover within 500 m of each wetland were estimated using a geographic information system. We chose a 500-m radius because amphibians have been shown, in other studies in agricultural landscapes, to have a core zone of about 300 m (Semlitsch and Bodie 2003) but at times travel farther, up to 1 km from the wetland (Pember et al. 2002; Porej et al. 2004; Swanson et al. 2018a). Using a combination of these, and additional variables identified by Sundberg et al. (2016) to be reliable condition indicators, a WCI score of 1–5 (1 = poor, 5 = good) was given to each wetland as an overall rating of wetland health. Variables were assigned to one of three categories: land cover descriptions, physical metrics, and biological metrics. Each category was given a rating and the total WCI score was calculated by averaging ratings from all three categories (Stewart et al. 2016; Sundberg et al. 2016). Air temperature (°C) was recorded at the end of each anuran survey along the wetland edge.

Data Analysis

To investigate environmental factors hypothesized to influence the presence of anurans, we examined both site- and landscape-level characteristics using an occupancy framework (MacKenzie et al. 2002). Bailey and Adams (2005: 5) define occupancy as "the proportion of sites, patches, or habitat units occupied by a species." Survey data were analyzed using single-season occupancy models accounting for detection probabilities <1 using Program MARK (v6.1; White and Burnham 1999; MacKenzie et al. 2002, 2006; MacKenzie and Bailey 2004). Occupancy modeling allows the use of detection data to estimate two parameters: the probability of detection given that a site is occupied (p) and the probability of occupancy (ψ). It can be used to understand how environmental factors influence the likelihood of a species inhabiting a site despite imperfect detection (Scott et al. 2002). We fit models to estimate p and ψ, and to test our hypotheses for each species and life stage, in 2015 and 2016. We report estimates (± 1 SD) for detection probability and site occupancy from the best model for all species and life stages. We analyzed 2015 and 2016 data separately because: (1) we were not interested in colonization or extinction parameters, (2) site-level environmental covariates were measured only in 2015, and (3) we were concerned the multi-season model would be problematic for a 2-yr study. We also analyzed life stages separately because habitat requirements vary among life stages for the same species.

Probability of detection.—Model selection was performed in two steps (MacKenzie et al. 2006). First, we assessed models to estimate detection probability (p). We built models that allowed p to (1) stay constant over the season, p(.); (2) vary independently among survey occasions p(t); (3) vary over the season by time (i.e., day of the year) with a linear trend, p(T); or (4) vary over the season by time (i.e., day of year) with a quadratic trend, p(TT). We also built additive models that included survey-specific air temperature (Temp) or percentage of aquatic vegetation cover (Veg) as interactive effects on t, T, and TT models (16 models; Appendix S2 in the Supplemental Materials available online). For the 2016 data, the six models including the vegetation covariate Veg were omitted (no data collected in 2016), resulting in fewer models for p in 2016 (10 models; Appendix S2). We used Akaike's information criterion (Akaike 1973) corrected for small sample sizes (AIC_c) to determine which models were best supported by the data.

TABLE 2.—Mean values (±1 SD) and ranges for environmental covariate data collected in north-central Iowa in 2015. See Appendix S4 (in the Supplemental Materials available online) for site-specific covariate values. Metrics for fish and salamander abundance are measured in number of individuals (*n*) and aquatic invertebrate density is recorded in number of individuals/m^3. Aquatic vegetation cover is measured as percentage of total open water cover, and cropland at 500 m indicates percentage of land use calculated within a 500-m radius of the wetland edge.

Covariate	Mean ± 1 SD	Range
Wetland condition index (score 1–5)	3.1 ± 1.1	1.5–4.6
Fish abundance (*n*)	1553 ± 4208	0–19,856
Salamander abundance (*n*)	20 ± 27	0–88
Aquatic vegetation cover (%)	85 ± 18	27–98
Aquatic invertebrate density (n/m^3)	363 ± 316	37–1291
Wetland area (ha)	2.1 ± 2.0	0.3–8.4
Atrazine concentration (μg/L)	0.7 ± 2.5	0.1–13.0
Cropland 500-m radius (%)	33 ± 17	0–72

The model structure(s) on *p* with a $\Delta AIC_c < 2$ were retained and used subsequently in our assessment of occupancy.

Probability of occupancy.—We built a set of models to estimate the probability of occupancy for each species and life stage using the model structure(s) that was supported for detection probability. We hypothesized that eight site- and landscape-level covariates (Table 1) would influence the probability of occupancy. We assessed models where occupancy was constant (i.e., no covariates, ψ[.]) and models that included one or two of the eight covariates (2015 data only) using the combinations approach (Doherty et al. 2012). For example, after building models to estimate occupancy on the detection probability model structure *p*(T), we had a set of 37 models (Appendix S3 in the Supplemental Materials, available online). Before analysis we used a correlation matrix generated with R (v3.3.3; R Core Team 2017) to ensure none of our eight covariates were highly correlated ($r > 0.60$; Amburgey et al. 2014).

On account of model selection uncertainty for some species, we performed a variable weights estimation using our list of candidate models to determine which two covariates were most important for each species and life stage (Burnham and Anderson 2003). Variable weights estimation determines which covariates exert the greatest influence on occupancy relative to one another when model selection is uncertain by summing the AIC_c weights of all models containing each covariate in a balanced model set. By calculating variable weights, we were able to compare the cumulative AIC_c weights of each environmental covariate and determine which covariates were the most influential for occupancy relative to one another. Some parameters (*p* or ψ) were not well estimated if they approached a parameter boundary (estimates near 0 or 1.0). We used Markov chain Monte Carlo estimation on the model with the best support for each species and life stage to obtain estimates of detection and occupancy parameters (White et al. 2006).

RESULTS

We conducted four surveys at 27 wetlands ($n = 108$ surveys) in 2015 and three surveys at the same 27 wetlands ($n = 81$ surveys) in 2016. Across both years we detected the presence of at least one life stage of *A. americanus* and *L. pipiens* at all wetlands (100%), *Hyla* spp. at 22 wetlands (81%), and *P. maculata* at 26 wetlands (96%; Appendix I). Environmental covariates were collected in 2015 only (Table 2). Some species and life stages were excluded from analysis because of nondetections, or because too few sites were occupied (i.e., egg masses of all species, metamorphs of *Hyla* spp. and *P. maculata*, and *P. maculata* adults in 2015).

Probability of Detection

In both years, the probability of detection for all species and life stages was influenced by time except for *A. americanus* metamorphs and *Hyla* spp. adults in 2015, which had constant detection probabilities. The influence of temperature was supported for *A. americanus* adults in 2015, *Hyla* spp. adults and tadpoles in 2016, and *P. maculata* tadpoles in 2016. The aquatic vegetation cover covariate received little support from the data, although the influence of this covariate was supported for *L. pipiens* tadpoles in 2015 (Table 3). The estimated influences of models

TABLE 3.—The most supported model (lowest AIC_c) for each species, life stage, and year in Iowa during 2015 and 2016. ψ = estimate of occupancy probability (±1 SD). Akaike's information criterion corrected for small sample sizes (AIC_c) = the relative measure of model support, *w* = model weight, and *k* = the number of parameters in a model. *Hyla* spp. is comprised of the *H. versicolor* and *H. chrysocelis* complex; see Appendix II for all supported models ($\Delta AIC_c < 2$).

Species	Life stage	Year	Model	ψ	AIC_c	*w*	*k*
Anaxyrus americanus	Adult	2015	p(T + Temp)ψ(WCI, Invert)	0.86 (± 0.12)	87.49	0.31	6
		2016	p(TT)ψ(.)	0.91 (± 0.07)	75.73	0.28	4
	Metamorph	2015	p(.)ψ(Crop, Fish)	0.45 (± 0.20)	49.85	0.24	4
		2016	p(t)ψ(.)	0.64 (± 0.18)	63.03	0.43	4
	Tadpole	2015	p(TT)ψ(Veg, Fish)	0.80 (± 0.13)	90.2	0.19	6
		2016	p(T)ψ(.)	0.76 (± 0.17)	52.89	0.33	3
Hyla spp.	Adult	2015	p(.)ψ(Crop, Fish)	0.61 (± 0.16)	90.38	0.31	4
		2016	p(T × Temp)ψ(.)	0.68 (± 0.20)	45.46	0.69	6
	Tadpole	2015	p(TT)ψ(Atrazine, Fish)	0.51 (± 0.11)	60.04	0.24	6
		2016	p(T + Temp)ψ(.)	0.23 (± 0.09)	34.84	0.66	4
Lithobates pipiens	Adult	2015	p(t)ψ(Area)	0.89 (± 0.06)	141.33	0.04	6
		2016	p(TT)ψ(.)	0.95 (± 0.04)	97.41	0.29	4
	Metamorph	2015	p(T)ψ(.)	0.94 (± 0.04)	56.46	0.08	3
		2016	p(TT)ψ(.)	0.91 (± 0.05)	59.47	0.29	4
	Tadpole	2015	p(TT + Veg)ψ(Sal)	0.91 (± 0.07)	94.47	0.13	6
		2016	p(t)ψ(.)	0.77 (± 0.14)	76.18	0.32	4
Pseudacris maculata	Adult	2016	p(T)ψ(.)	0.70 (± 0.19)	37.95	0.53	3
	Tadpole	2015	p(TT)ψ(WCI, Crop)	0.94 (± 0.05)	89.05	0.06	6
		2016	p(t ×Temp)ψ(.)	0.68 (± 0.21)	50.45	0.21	5

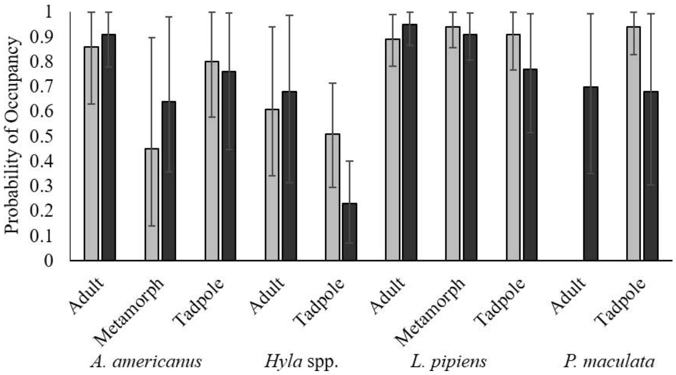

Fig. 2.—Amphibian occupancy by species and life stage in Iowa during 2015 (light gray) and 2016 (dark gray). *A. americanus* = *Anaxyrus americanus* (American Toads); *Hyla* spp. = *Hyla versicolor* and *Hyla chrysocelis* (Gray Treefrogs and Cope's Gray Treefrogs, respectively); *L. pipiens* = *Lithobates pipiens* (Northern Leopard Frogs); and *P. maculata* = *Pseudacris maculata* (Boreal Chorus Frogs). Error bars represent 95% confidence intervals. Estimates are from the model with the most support (see Table 3).

including either temperature or vegetation as a covariate were very weak and not significant (95% confidence intervals [CIs] included zero), and likely did not drive detection.

Probability of Occupancy

Occupancy varied by species and life stage. In 2016, *Hyla* spp. tadpoles had the lowest probability of occupancy (0.23 ± 0.09) while *L. pipiens* had the highest probability of occupancy (0.95 ± 0.04; Table 3; Fig. 2). Occupancy estimates were similar between years for each species and life stage, with the greatest differences between tadpoles of the *Hyla* spp. (0.51 ± 0.11 in 2015 and 0.23 ± 0.09 in 2016) and *P. maculata* (0.94 ± 0.05 in 2015 and 0.68 ± 0.21 in 2016; Table 3; Fig. 2).

Results from the variable weights estimation showed that all covariates (except aquatic invertebrate density) were among the top two most influential covariates for at least one species and life stage. Fish abundance, surrounding crop cover, and salamander abundance covariates influenced occupancy of several species and life stages (Table 4). Wetland area, atrazine concentration, vegetative cover, and WCI also influenced occupancy probability, but each of these covariates was influential for only a single species and life stage (e.g., WCI was among the top two most influential covariates for only *P. maculata* tadpoles; Tables 4, 5).

Discussion

In modified habitats where amphibians persist, it is important to determine how environmental factors influence their presence. Understanding the relationship that amphibians have with their environment in agricultural landscapes could help to effectively manage these areas to the advantage of amphibians. The focus of this study was to determine the presence of anuran species in wetlands in an agricultural landscape and explore the influence of site characteristics on occupancy. We estimated detection and occupancy probability for four anuran species in northern Iowa.

The top models included covariates that influenced occupancy for all species and life stages, but none of them were supported strongly (i.e., 95% CI of each model coefficient included zero). Despite this lack of strong support for covariates, the direction of the trend in most cases matched our hypotheses (which are supported by previous work; e.g., Babbitt et al. 2003; Knutson et al. 2004; Hartel et al. 2007; Amburgey et al. 2014). Our results indicate that there is biological relevance to our selected covariates, but data from a greater number of sites, where species occupancy is more variable, are needed to help clarify putative effects. Additional years of survey data could also strengthen potential relationships tested in the models.

Fish are known predators of amphibians and their presence is often a strong indicator of occupancy (Hecnar and M'Closkey 1997; Hero et al. 1998). Although fish abundance was one of the top two covariates in four of our model sets, model coefficients estimating influence were near zero (<0.01). Of the 27 wetlands studied, fish known to be predators of anurans were present in only three (Hecnar and M'Closkey 1997). Two sites contained Black Bullheads (*Ameiurus melas*) and Green Sunfish (*Lepomis cyanellus*), while the other site was in proximity to a river and contained Bullheads, Sunfish, and Northern Pikes (*Esox lucius*). By far, the two most common fish species detected at our wetlands were Brook Sticklebacks (*Culaea inconstans*) and Fathead

Table 4.—Results of variable weights estimation on anuran occupancy in Iowa in 2015. Each column represents a species and life stage. A = Adult, M = Metamorph, T = Tadpole. Values show the weight given to each covariate relative to one another, and indicate their relative influences on the probability of occupancy. The two most influential covariates for each species and life stage are indicated in bold. *Hyla* spp. represents the *H. versicolor* and *H. chrysocelis* complex; area = area of wetland (ha); atrazine = concentration of atrazine detected in wetland (μg/L); crop = percentage of land use in corn or soybeans calculated within a 500-m radius of the wetland edge; fish = fish abundance (number of individuals); invert = aquatic invertebrate density (number of individuals/m^3); sal = salamander abundance (number of individuals); veg = aquatic vegetation cover (percentage of total wetland cover); and WCI = wetland condition index values (Score 1–5).

	Anaxyrus americanus			*Hyla* spp.		*Lithobates pipiens*			*Pseudacris maculata*
Covariate	A	M	T	A	T	A	M	T	T
Area	0.15	0.04	0.07	0.01	0.05	**0.32**	0.16	0.19	0.17
Atrazine	0.03	0.05	0.07	0.03	**0.41**	0.08	0.12	**0.31**	0.07
Crop	**0.46**	**0.59**	0.09	**0.81**	0.04	0.09	**0.19**	0.08	**0.35**
Fish	0.22	**0.87**	0.34	**0.96**	**0.92**	**0.30**	0.19	0.08	0.27
Invert	0.35	0.04	0.13	0.04	0.12	0.12	0.12	0.11	0.10
Sal	0.09	0.11	**0.37**	0.02	0.11	0.28	**0.23**	**0.51**	0.08
Veg	0.09	0.04	**0.50**	0.05	0.12	0.15	0.13	0.19	0.30
WCI	**0.42**	0.07	0.15	0.02	0.07	0.15	0.14	0.11	**0.31**

TABLE 5.—Estimates of model coefficients with corresponding 95% confidence interval for the two most influential covariates determined by variable weights estimation for each species and life stage in Iowa in 2015. Direction of predicted effect (positive [+] or negative [−] = hypothesized relationship between the covariate and occupancy probability [ψ]). *Hyla* spp. represents the *H. versicolor* and *H. chrysoscelis* complex; A = adult; M = metamorph; T = tadpole; Area = area of wetland (ha); Atrazine = concentration of atrazine detected in wetland (μg/L); Crop = percentage of land in corn or soybeans within a 500-m radius of the wetland edge; Fish = number of individual fish; Invert = aquatic invertebrate density (number of individuals/m^3); Sal = number of individual salamanders; Veg = aquatic vegetation cover (percentage of total open water cover); WCI = wetland condition index value (Score 1–5).

Covariate	Predicted effect on ψ	*Anaxyrus americanus* A	*Anaxyrus americanus* M	*Anaxyrus americanus* T	*Hyla* spp. A	*Hyla* spp. T	*Lithobates pipiens* A	*Lithobates pipiens* M	*Lithobates pipiens* T	*Pseudacris maculata* T
Area	+						0.17 (−0.17, 0.52)			
Atrazine	−					0.07 (−0.13, 0.30)			−0.04 (−0.31, 0.25)	
Crop	−	1.27 (−1.82, 4.40)	0.66 (−2.63, 3.28)		−0.20 (−3.38, 3.00)			1.12 (−2.02, 4.22)		−0.05 (3.35, 3.03)
Fish	−		<0.01 (<−0.01, <0.01)		< −0.01 (< −0.01, < 0.01)	<0.01 (< −0.01, < 0.01)	<0.01 (< −0.01, < 0.01)			
Invert	+									
Sal	−			−0.02 (−0.05, 0.01)				0.01 (−0.03, 0.04)	< −0.01 (−0.04, 0.04)	
Veg	+			0.12 (−2.85, 3.34)						
WCI	+	0.04 (−0.65, 0.83)								0.36 (−0.28, 0.97)

Minnows (*Pimephales promelas*). Both species are planktivorous and do not to influence anurans by direct predation (Coyle 1930; Tompkins and Gee 1983). Although they might alter wetland ecosystems by changing oxygen levels or vegetation communities, Herwig et al. (2013) showed that planktivores alone had very little effect on ranid tadpoles (e.g., *L. pipiens*).

Bullfrogs (*Lithobates catesbeianus*) are known predators of other ranid frogs and negatively affect certain amphibian species (e.g., Pearl et al. 2004). Bullfrogs were detected at only five wetlands and so were not included as a covariate. Furthermore, all other anuran species were detected at those five sites, with the exception of *Hyla* spp. at two sites. However, range expansion of bullfrogs into parts of Iowa not occupied historically might become an increasingly important cause of decline in other amphibian species (Christiansen and Bailey 1991).

Contrary to our hypotheses, the percentage of cropland cover within a 500-m radius of each wetland had a positive influence on *A. americanus* adults and metamorphs and *L. pipiens* metamorphs. In our study area, agriculture is primarily annual row crops (i.e., corn and soybeans) that are typically rotated between years. Although we predicted a negative effect, in agricultural wetlands in Minnesota, Knutson et al. (2004) did not find a negative effect on amphibians living in ponds surrounded by row crops relative to amphibians living in ponds surrounded by nongrazed pasture. It is possible that we did not see a negative effect of surrounding crop cover on *A. americanus* because they are more resilient to desiccation compared to many frog species (Green 2005).

We hypothesized that atrazine would have a negative influence on site occupancy by anurans. Although this hypothesis was supported for *L. pipiens* tadpoles, atrazine showed a positive influence on occupancy of *Hyla* spp. tadpoles. The observed concentrations of atrazine in our wetlands might not have been high enough to affect site occupancy. Hayes et al. (2003) reported that atrazine concentrations up to 200 μg/L did not affect larval mortality directly, nor did it affect time to metamorphosis, length, or mass at metamorphosis. The mean atrazine concentration at our sites was 0.7 μg/L (SD = 2.5). Even at low concentrations, however, atrazine has the potential to negatively affect amphibian health, which would not be revealed by an occupancy analysis (Hayes et al. 2003; Mann et al. 2009).

We included an overall measure of wetland health (the WCI) as a covariate. We found that the presence of *P. maculata* tadpoles had a positive association with wetlands with high WCI values, but a high WCI score was not a reliable indicator for presence of the majority of amphibian species and life stages. The WCI is representative of overall wetland condition, which is an essential metric to consider for general wildlife diversity at wetlands (Stewart et al. 2016). Our results show, however, that it might be too general a measure to capture the attributes that are of greatest relevance to anuran occupancy. For example, managers seeking to conserve a particular species of interest, or a suite of amphibian species, might find it more useful to focus on individual environmental factors rather than an overall measure of site condition.

Conclusions

We documented high site occupancy by anuran amphibians in highly modified agricultural landscapes but were unable to identify specific environmental characteristics that might be driving variation in occupancy. Despite equivocal support for our hypotheses, our data reflected the potential for most of the covariates that we assessed to affect occupancy in ways that we predicted. We found that amphibians occurred and bred in wetlands in a highly modified agricultural landscape, but we note that our study did not estimate the survival or health of individuals or populations. Occupancy analyses conducted over a greater period of time, or research designed specifically to assess survival and health would complement information gathered in this study.

Despite resilience shown by the occupancy of anuran species in modified landscapes in this study, amphibian populations in the Midwestern United States are experiencing overall declines (Grant et al. 2016). Whereas the populations in our study area might be relatively tolerant to the conversion of natural landscapes to agriculture, they may still be in the process of responding to effects of our measured environmental covariates. For example, Green Frogs (*Lithobates clamitans*) and Cricket Frogs (*Acris crepitans*) might have occurred historically at some our study sites (Christiansen and Bailey 1991), but could have been extirpated because greater sensitivity to the wide-scale land use changes in Iowa. This suggests that with management, including restoration or protection of amphibian habitats within agricultural landscapes, a more diverse community of amphibians could be supported.

Our results lay a foundation for understanding how amphibians are using landscapes that have undergone modification. Although amphibian occurrence is thought to have an association with overall wetland quality, our study did not reveal strong evidence that a high WCI was associated with increased amphibian occupancy. In a highly modified landscape such as Iowa, the greatest obstacle in identifying environmental characteristics that drive amphibian occupancy might be the artificial landscape homogenization. In this landscape, amphibians might use any area of available habitat, even suboptimal habitat, out of necessity. This suggests that in areas of high agricultural land use, the addition of even small habitat patches might be beneficial to amphibian populations (e.g., providing resources to facilitate dispersal; Watts et al. 2015). Our study demonstrates the ability of anuran populations to persist in a highly modified environment in concurrence with potentially harmful environmental characteristics, and provides insight into the use of agricultural habitats by amphibians.

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Supplemental Material

Supplemental material associated with this article can be found online at https://doi.org/10.1655/Herpetologica-D-18-00013.S1 (see also Swanson et al. 2018b).

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Appendix I

Naïve proportion of sites occupied by anuran species and life stages in Iowa during surveys occurring in 2015 and 2016. *Hyla* spp. represents the *H. versicolor* and *H. chrysocelis* complex.

Species	Life stage	2015	2016
Anaxyrus americanus	Adult	16/27 (59%)	21/27 (78%)
	Metamorph	6/27 (22%)	11/27 (41%)
	Tadpole	17/27 (63%)	9/27 (33%)
	Egg	1/27 (4%)	2/27 (7%)
Hyla spp.	Adult	12/27 (44%)	7/27 (26%)
	Metamorph	3/27 (11%)	0/27 (0%)
	Tadpole	13/27 (48%)	5/27 (19%)
	Egg	0/27 (0%)	0/27 (0%)
Lithobates pipiens	Adult	24/27 (89%)	26/27 (96%)
	Metamorph	26/27 (96%)	25/27 (93%)
	Tadpole	21/27 (78%)	14/27 (52%)
	Egg	0/27 (0%)	4/27 (15%)
Pseudacris maculata	Adult	1/27 (4%)	7/27 (26%)
	Metamorph	1/27 (4%)	1/27 (4%)
	Tadpole	24/27 (89%)	7/27 (26%)
	Egg	0/27 (0%)	0/27 (0%)

Appendix II

Supported occupancy models ($\Delta AIC_c < 2$) for each anuran species and life stage sampled in Iowa in 2015. ΔAIC_c = the change in Akaike's information criterion corrected for small sample sizes (AIC_c) from most supported model and k = number of parameters. *Hyla* spp. represents the *H. versicolor* and *H. chrysocelis* complex; for descriptions of models, see examples presented in Appendix S3 of the Supplemental Materials available online.

Species	Life stage	Model name	ΔAIC_c[1]	*k*	Deviance
Anaxyrus americanus	Adult	p(T + Temp)ψ(WCI, Invert)	0.00	6	71.29
		p(T + Temp)ψ(Crop, Fish)	0.98	6	72.27
	Metamorph	p(.)ψ(Crop, Fish)	0.00	4	40.03
		p(T)ψ(Crop, Fish)	0.98	5	37.98
		p(T + Veg)ψ(WCI, Crop)	1.32	3	44.13
	Tadpole	p(TT)ψ(Veg, Fish)	0.00	6	74.00
		p(TT)ψ(Sal)	1.68	5	79.02
		p(TT)ψ(Veg)	1.75	5	79.09
		p(TT)ψ(Veg, Invert)	1.83	6	75.83
Hyla spp.	Adult	p(.)ψ(Crop, Fish)	0.00	4	80.57
		p(TT)ψ(Crop, Fish)	0.35	6	74.54
		p(T)ψ(Crop, Fish)	1.25	5	78.78
	Tadpole	p(TT)ψ(Atrazine, Fish)	0.00	6	43.84
		p(T)ψ(Atrazine, Fish)	0.95	5	48.13
	Adult	p(t)ψ(Area)	0.00	6	125.13
		p(t)ψ(.)	0.26	5	128.73
		p(t)ψ(Fish, Sal)	0.49	7	121.93
		p(TT)ψ(Area)	0.56	5	129.03
		p(t)ψ(Area, Fish)	0.67	7	122.10
		p(t)ψ(Fish)	0.72	6	125.85
		p(TT)ψ(Fish, Sal)	0.81	6	125.94
		p(TT)ψ(.)	0.89	4	132.40
		p(TT)ψ(Area, Fish)	0.98	6	126.11
		p(×Temp)ψ(.)	1.03	6	126.16
		p(×Temp)ψ(Area)	1.06	7	122.50
		p(t)ψ(Veg, Sal)	1.41	7	122.85
		p(t)ψ(Area, Sal)	1.66	7	123.10
		p(TT)ψ(Veg, Sal)	1.70	6	126.83
		p(×Temp)ψ(Fish)	1.73	7	123.17
		p(t)ψ(WCI)	1.74	6	126.87
		p(×Temp)ψ(Fish, Sal)	1.87	8	119.20
		p(t)ψ(WCI, Sal)	1.89	7	123.33
		p(TT)ψ(Area, Sal)	1.94	6	127.07
		p(t)ψ(Sal)	1.96	6	127.09
	Metamorph	p(T)ψ(.)	0.00	3	49.42
		p(T + Temp)ψ(.)	1.41	4	48.05
		p(T + Veg)ψ(.)	1.46	4	48.10
Lithobates pipiens		p(T)ψ(Crop)	1.74	4	48.38
		p(T)ψ(Fish)	1.74	4	48.38
		p(T)ψ(Sal)	1.79	4	48.43
		p(T)ψ(Area)	1.94	4	48.58
	Tadpole	p(TT + Veg)ψ(Sal)	0.00	6	78.27
		p(TT))ψ(Veg, Area)	1.20	6	79.47
		p(TT)ψ(Atrazine, Sal)	1.20	6	79.47
		p(TT)ψ(Atrazine)	1.48	5	83.09
		p(TT)ψ(Sal)	1.48	5	83.09
Pseudacris maculata	Tadpole	p(TT)ψ(WCI, Crop)	0.00	6	72.85
		p(TT)ψ(WCI, Area)	0.00	6	72.85
		p(TT)ψ(Veg, Crop)	0.00	6	72.85
		p(TT)ψ(Veg, Fish)	0.00	6	72.85
		p(TT + Temp)ψ(WCI, Crop)	1.02	7	70.17
		p(TT + Temp)ψ(WCI, Area)	1.02	7	70.17
		p(TT + Temp)ψ(Veg, Crop)	1.02	7	70.17
		p(TT + Temp)ψ(Veg, Fish)	1.02	7	70.17
		p(TT + Temp)ψ(Crop)	1.09	6	73.94
		p(TT + Temp)ψ(Fish)	1.09	6	73.94
		p(TT)ψ(Veg)	1.76	5	77.95
		p(TT)ψ(Fish)	1.76	5	77.95
		p(TT)ψ(Invert)	1.76	5	77.95

[1] The AIC_c value of the top model for *A. americanus* adults = 87.49, metamorphs = 49.85, tadpoles = 90.20; *Hyla* spp. adults = 90.38, tadpoles = 60.04; *L. pipiens* adults = 141.33, metamorphs = 56.46, tadpoles = 94.47; and *P. maculata* tadpoles = 89.05.