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Managing farm ponds as breeding sites for amphibians: key trade-offs in agricultural function and habitat conservation

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Abstract. Millions of farm ponds have been constructed in agricultural landscapes around the globe. These ponds are built to support a variety of functions, including erosion control, cattle grazing, and recreational fishing, but their role as breeding habitat for amphibians remains poorly understood. We addressed this knowledge gap by studying farm ponds in the eastern Great Plains of the United States, a pond-dense region dominated by agriculture. We used field surveys and occupancy modeling to identify the important biophysical components of amphibian habitat and to assess the species-specific effects of cattle and fish presence on breeding occupancy. We next used a chronosequence to determine whether pond renovation, which often occurs when ponds are about 40 yr old, threatens the development of amphibian habitat. Nine amphibian species bred in the farm ponds that we surveyed, and the relationship between breeding occupancy and habitat variables varied by species. We found that the pH conditions associated with amphibian breeding occupancy were significantly more likely to occur in older ponds (>50 yr old). Emergent vegetation cover was also associated with increased breeding probability and rarely reached high levels in newer ponds. Since the older ponds with suitable habitat are at an age where renovation is likely needed to restore their agricultural function, this habitat may be at risk. We suggest that conservation of amphibians in farm ponds in the United States will require adopting renovation and management practices that balance the multiple uses of these sites and maintain a mosaic of pond successional states.

Key words: agriculture; amphibians; farm dams; farm ponds; management; novel ecosystems; reconciliation ecology; wetlands.

Introduction

Conversion of land to support agriculture is frequently accompanied by severe loss of biodiversity (Global Biodiversity Outlook 2010). However, biodiversity can persist even in highly altered landscapes if suitable anthropogenic habitat is available (Lundholm and Richardson 2010, Fahrig et al. 2011). Under the framework of reconciliation ecology, ecologists are tasked with promoting biodiversity conservation in these landscapes "where people live, work, or play" (Rosenzweig 2003). Farm ponds, which number in the millions in the agricultural landscapes of the United States (Renwick et al. 2006, Chumchal et al. 2016), present one often overlooked opportunity to do so (Downing 2010, Hill et al. 2018). While farm ponds worldwide have been shown to support a suite of organisms including waterbirds (Sebastián-González et al. 2010), songbirds (Lewis-Phillips et al. 2019), aquatic macroinvertebrates (Brainwood and Burgin 2009), and amphibians (Knutson et al. 2004), in the United States they are typically designed and managed to perform a narrow range of agricultural functions (Renwick et al. 2005, Chumchal and Drenner 2015). As a result, their vital role in bolstering populations of vulnerable taxa, like amphibians, remains underappreciated (Knutson et al. 2004, Chester and Robson 2013) and opportunities to conserve biodiversity while maintaining the agricultural functions of ponds are unidentified (but see Huggins et al. 2017).

In the U.S. Great Plains, providing water for livestock on grazing lands is a primary motivation for constructing farm ponds (Renwick et al. 2006, Chumchal and Drenner 2015). Many ponds also serve secondary functions like providing recreational fishing opportunities, irrigation, and erosion control (Compton 1952, Hawley 1973, Renwick et al. 2006). Management for these functions affects habitat structure in ways important to amphibians. For example, to ensure that ponds can serve these functions even during periods of low precipitation,

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they usually have deep basins and steep banks (Chumchal and Drenner 2015). Though this design maximizes water retention capacity (Compton 1952), it may be problematic for many amphibians (Leja 1998, Shulse et al. 2010). Steep banks can reduce the availability of the shallow, vegetated littoral zones that provide habitat for foraging, oviposition, and refuge from predators (Knutson et al. 2004, Porej and Hetherington 2005, Shulse et al. 2010). Vegetation presence and other factors can in turn influence pond pH (Mitsch and Gosselink 2015), which can affect larval development and recruitment (Sparling 2010). It is also recommended that cattle be excluded from ponds with fences (Giuliano 2006), since they can have direct negative impacts on pond habitat: they can trample pond shallows and uproot or graze wetland vegetation (Trimble 1994, Trimble and Mendel 1995, Jansen and Healey 2003). These cattle-mediated effects can in turn lead to reductions in amphibian species richness and reproductive success (Knutson et al. 2004, Marty 2005).

Management of ponds to provide recreational fishing opportunities could pose additional challenges for amphibian populations (Leja 1998, Knutson et al. 2004). In the United States, gamefish introductions to ponds have been widespread since the 1950s (Compton 1952, Hawley 1973, Leja 1998). While sunfish (*Lepomis* spp.) and largemouth bass (*Micropterus salmoides*) provide anglers with recreational opportunities, these species can be voracious predators of amphibian eggs and larvae (Kats et al. 1988, Kats and Ferrer 2003). Depending on the amphibian species of interest, gamefish introductions may not be compatible with amphibian conservation (Hartel et al. 2007). Facilitating the establishment of these predators may be a key way in which landowners affect amphibian populations.

Pond owners can also impact habitat availability by interfering with successional processes when renovating older ponds. As ponds age, their basins can accumulate sufficient sediment such that they become shallow, unreliable, water sources (Chumchal and Drenner 2015, Chumchal et al. 2016). This results in decreased agricultural function that must be restored through pond renovation, which entails draining and dredging the pond. In the process of resetting the ecological and agricultural status of the ponds, renovation also destroys in-pond habitat linked to succession (e.g., vegetation establishment and growth). Depending on the timing of amphibian habitat succession, renovation may eliminate existing habitat or even entirely prevent the development of suitable habitat. In southern Iowa, ponds typically need to be renovated at 40 yr old, conditional on watershed use (Adam Gottemoeller, *personal communication*). How renovating 40 yr old ponds impacts the availability of amphibian habitat remains a key gap in our understanding of the effects of pond management on amphibians.

In this study, our goal was to assess habitat associations of farm pond amphibian species and evaluate the effect of management actions on habitat availability and development. We studied ponds in the northernmost part of the pond-dense region that extends from central Texas to southern Iowa along the eastern edge of the U.S. Great Plains (see Chumchal and Drenner 2015), a region we refer to as the "pond belt." Natural wetlands were historically scarce in our study region, and farm ponds now comprise the vast majority of lentic habitat available (Gallant et al. 2011). To understand how management affects amphibians using these ponds, we first used occupancy modeling to identify species-specific predictors of amphibian reproduction, including cover of wetland vegetation, pond slope, and water quality. We then constructed a chronosequence using historical aerial photos to understand the sequence of habitat development and assess whether renovating ponds threatens amphibian habitat. We hypothesized that ponds without cattle or predatory fish, with gently sloping littoral zones, and with high levels of wetland vegetation would be more likely to be occupied by amphibian larvae. We also expected that amphibians would prefer ponds with a circumneutral pH. We hypothesized that older ponds (>40 yr old) would generally possess more of the characteristics associated with amphibian breeding use. Suitable breeding sites would thus be at risk of renovation. By identifying habitat characteristics predictive of amphibian breeding activity and establishing the sequence of habitat development with reference to pond renovation, we provide a path forward for incorporating amphibian conservation into the existing functions of farm ponds in agricultural landscapes.

Methods

Study area

We conducted this study on ponds located on public lands in Ringgold County, Iowa, within the Grand River Grasslands (Fig. 1), a focal region for ongoing efforts to restore a functioning tallgrass prairie ecosystem spanning public and private lands (The Nature Conservancy 2012). Historical aerial imagery shows that ponds have been constructed on farmland throughout the region since at least the 1930s, and Ringgold County now boasts the highest density of farm ponds in Iowa (>4 ponds/km^2; T. Swartz, *unpublished data*). We sampled ponds on the Kellerton Bird Conservation Area and the Ringgold Wildlife Management Area, which are protected areas owned by the Iowa Department of Natural Resources (IDNR). Now managed for wildlife conservation, these areas were historically privately owned farmland. In addition to ponds built more recently, they contain numerous ponds built prior to their acquisition by the IDNR. These areas provide an opportunity to study ponds along a spectrum of successional stages (Fig. 2), including older ponds that are now scarce on adjacent private lands (T. Swartz, *unpublished data*).

Agricultural activities, like cattle grazing and row crop production, persist in both areas today, though it is now

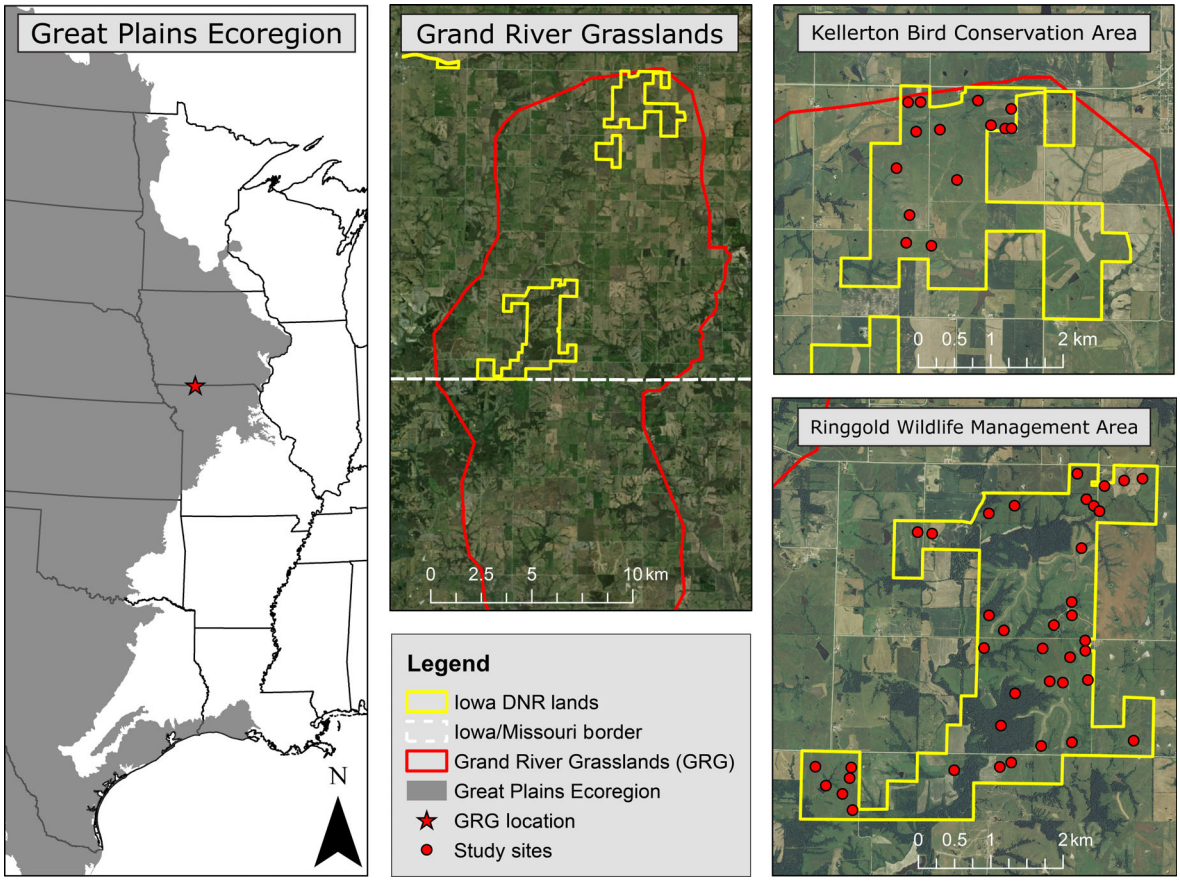

FIG. 1. Location of study sites (n = 51) in the Grand River Grasslands of the eastern Great Plains in southern Iowa, USA. Sites were located on two parcels managed by the Iowa Department of Natural Resources: the Kellerton Bird Conservation Area and the Ringgold Wildlife Management Area.

more limited and is carefully overseen by the IDNR. Like much of the surrounding landscape, the Kellerton Bird Conservation Area and the Ringgold Wildlife Management Area are both dominated by grassland, though the latter also contains some mixed-timber woodlands (about one-quarter of the area). Our sample (n = 51) included ponds located on pastures leased to local cattle producers to graze cattle (n = 16) as well as those located on ungrazed grasslands (n = 24) and within mixed hardwood forest (n = 11). Pond surface area was 1,468 ± 4,458.51 m^2 (mean ± SD). Climate in the region is characterized by hot summers (mean temperature 22.7°C) and cold winters (mean temperature −3.4°C), and average annual precipitation is 91 cm, with most (63%) of this precipitation occurring between May and September (PRISM Climate Group 2017).

Sampling design

We used a repeated sampling approach to determine the presence of breeding populations of amphibians at our study sites. Ponds were sampled up to four times per summer in 2016 and 2017. We surveyed each pond once per day during an initial 2-d period, beginning on 31 May. Ponds were then surveyed two more times during a second 2-d sampling period approximately 30 d later, if possible (e.g., ponds that no longer held water by the second sampling period were not resampled). For logistical reasons, ponds were sampled in clusters (determined by proximity), and the sampling order of clusters was randomized and differed across years. In both 2016 and 2017, 46 of the 51 ponds (90.2%) were sampled during both sampling periods.

During each sampling period, we surveyed ponds for evidence of amphibian reproduction (presence of larvae, metamorphs, or juveniles) and predatory fish presence using two types of funnel traps: collapsible polyethylene mesh hoop traps and modified steel minnow traps (see Swartz and Miller 2018), both of which are commonly used to sample predatory fish in amphibian studies (e.g., Shulse et al. 2010, and Cosentino et al. 2011). The number of traps deployed was proportional to pond perimeter. For ponds with perimeters < 50 m, we deployed four steel minnow traps and one collapsible hoop trap. An additional trap of each type was added for every 50-m increase in perimeter length. The median number

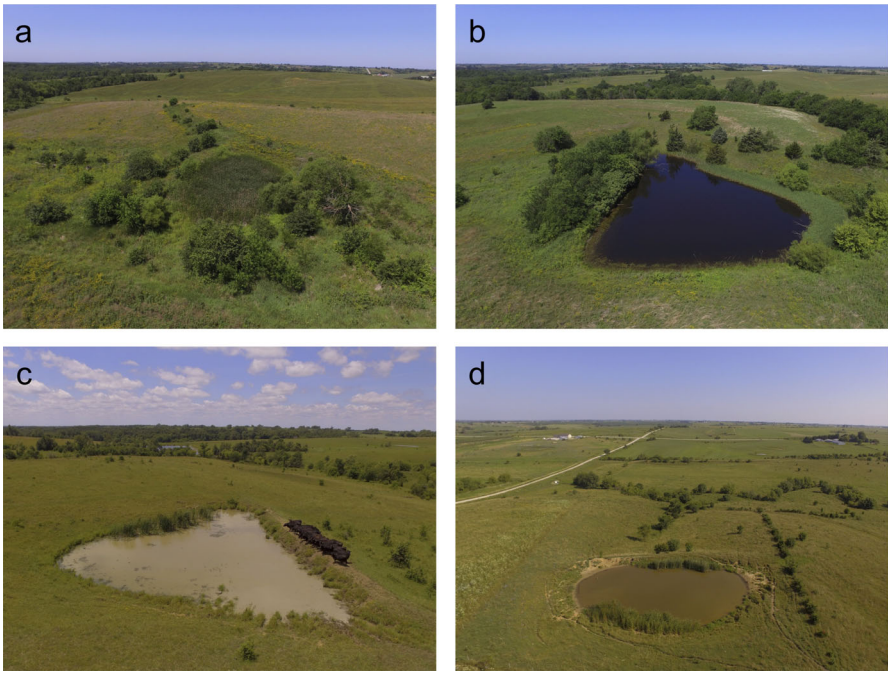

Fig. 2. Images depicting farm ponds included in our study of ponds in Ringgold County, Iowa, in the eastern U.S. Great Plains. Cover of emergent plants, like cattails, can be extensive in older farm ponds (a; constructed between 1954 and 1960). In newer ponds (b; constructed between 1966 and 1973), cattail cover is concentrated along the margins. Ponds located on grazed pastures may exhibit evidence of cattle use. Typically, cattle will create trails along the embankment or elsewhere along the pond margin (c). Emergent vegetation may also develop along the margins of ponds with cattle (d).

of traps deployed was nine (six minnow, three hoop). In some cases, mid-summer pond drying led to a decrease in shoreline length between sampling periods, and so fewer traps were deployed. Traps were evenly spaced along the shoreline and placed within 1 m of the water's edge. We checked traps every 24 h and recorded presence or absence of all species and life stages of amphibians and fish. We classified fish as predatory (centrarchids, eocids, and salmonids) or non-predatory (cyprinids), after Hecnar and M'Closkey (1997).

To assess how the habitat characteristics affect amphibian occupancy patterns, we measured several parameters in the littoral zones of each pond. These zones along the pond are important for amphibians, partly because hydrophytic plants can become rooted in the shallow water, which provides microhabitat (Porej and Hetherington 2005). During each of the first sampling periods in 2016 and 2017, we measured habitat variables at the cardinal (north, south, east, and west) and intercardinal directions (northeast, northwest, southeast, and southwest) along the pond perimeter. Vegetation cover of the pond littoral zone was sampled in quadrats (1 × 1 m) placed along the water's edge and extending into the pond. Quadrats were distributed around the pond perimeter at eight evenly spaced intervals. Within each quadrat we visually estimated percent cover, rounded to 5% cover classes, of three categories of vegetation based on growth habit: emergent vegetation (rooted plants with stems and leaves extending above the water's surface), submerged vegetation (plants with their biomass located below the surface), or floating vegetation (plants with most or all of their mass existing on the surface of the pond). At each quadrat location, we also measured pond depth at 1 m and 3 m along a transect perpendicular to the shoreline. We calculated within-wetland slope from these depths and averaged slope among quadrats. In 2017, we also measured water pH within each of the eight vegetation quadrats using an Oakton Instruments Multi-parameter PCSTestr 35 (Oakton Instruments, Vernon Hills, Illinois, USA). We used information from the IDNR and the lessees to determine whether cattle had access to each pond, and we verified this information during surveys.

Pond size and pond age estimation

We used ArcMap (v10.5; Environmental Systems Research Institute, Redlands, California, USA) to determine the area and perimeter of each pond using 3-m resolution RGB imagery (National Agricultural Imagery Program, United States Department of Agriculture, Farm Service Agency, 2015). Pond area was log-transformed for analyses. Using aerial imagery, we also calculated the proportion of the pond edge that was covered by woody vegetation by intersecting the pond perimeter with a digitized tree cover layer. We suspected

woody vegetation could also affect the trajectory of wetland succession since it can limit the light available to herbaceous wetland vegetation and affect plant productivity (Sayer et al. 2012).

We used historical aerial imagery to determine the approximate age of each pond and constructed a chronosequence of pond habitat development. Orthorectified imagery was acquired from the IDNR GIS Database and the digital archives from the University of Iowa (*available online*).[5,6] Aerial photographs of our study area were available for the following years: 1938, 1947, 1954, 1960, 1966, 1973, 1979, 1983, 1997, 2002, 2007, and 2015. We assigned ponds to age classes based on the acquisition year of imagery in which they first appeared, which resulted in the following five age classes: <30 (n = 11), 30–39 (n = 6), 40–49 (n = 9), 50–59 (n = 16), and > 60 (n = 9) years old.

In some cases (n = 10), it was evident that a pond had been renovated, as indicated by a change in pond size, location, or shoreline morphology between imagery periods. We assigned these ponds to the age class corresponding with their renovation date, not their year of initial construction, since renovated ponds and newly built ponds have very similar structure (open water, steep banks, and little to no hydrophytic vegetation). This approach allowed us to examine the sequence of habitat development from a baseline of the "disturbance" event that initiated current development, regardless of whether the pond was constructed or renovated. Assigning renovated ponds to the age class corresponding with their renovation year suited our purpose of evaluating the timing of habitat succession. However, had our focus been on directly linking renovation to amphibian use, a different approach may have been necessary to account for site fidelity behaviors, which lead some amphibians to return to breed in sites that have been substantially altered or even destroyed (e.g., Pechmann et al. 2001). Since only one of the ponds had been renovated within the 10 yr preceding the study period, the impact of these potential holdover effects was likely minimal.

Statistical analyses

We limited our breeding occupancy analyses to the summer-breeding species targeted by our sampling design. These focal species included Blanchard's cricket frog (*Acris blanchardi*), Cope's gray treefrog and eastern gray treefrog (*Hyla chrysoscelis* and *Hyla versicolor*, hereafter referred to as gray treefrogs since they are sympatric through much of their range, including our survey area (Oberfoell and Christiansen 2001), and cannot be reliably differentiated in the field [Altig and McDiarmid 2015]), plains leopard frog (*Lithobates blairi*), and American bullfrog (*L. catesbeianus*).

For each of the four species, we used data from multiple occupancy surveys to model detection and breeding occupancy in the package unmarked (Fiske 2011) in R v. 3.5.1 (the code used is available on Github; see *Data Availability*), which allowed us to account for imperfect detection. We determined breeding occupancy status based on the presence of any larval, metamorphic, or juvenile amphibians. We used single-season occupancy models to examine detection and breeding occupancy rates for each year of the study and to identify important variables associated with breeding occupancy. We did not combine our observations into a single encounter history spanning both years, as doing so would violate the assumption that populations remain closed to changes in occupancy status during the primary sampling periods (MacKenzie 2006).

We first conducted analyses to select a model that accounted for variation in detection rate while holding occupancy rate constant. Our candidate model set included two models without detection covariates; a base "constant" model, representing homogenous detection, and a fully time-varying model. We then generated three models with a single detection covariate each, either survey day within a sampling season (1–4), day of the year (calendar date of the survey day; 1 January = 1), or temperature (mean temperature on the survey day). Day of the year was included to account for changes in breeding activity across the sampling season and temperature was included to account for variation in larval activity or habitat use due to temperature. We generated two additive models with temperature and either survey day or day of the year and two models including an interaction of temperature with either survey day or day of the year. We used the Akaike information criterion corrected for small sample size (AIC_c) to rank models and select the best-supported detection model from our candidate set. We repeated this procedure for each species in each year. The detection model with the most support was carried forward as the base "null" model for modeling breeding occupancy.

To evaluate support for habitat parameters potentially influencing breeding occupancy, we adopted a two-stage approach intended to minimize the chance of selecting weakly supported, "uninformative" parameters (Arnold 2010). We first generated univariate models each containing one explanatory habitat variable (see Table 1) and the "base" model for detection. For each species, seven univariate models were generated in 2016 and eight in 2017, when we measured pH. From this candidate set, we considered all models present in the 95% confidence set to be competitive (cumulative Akaike weight [w_i]; Burnham and Anderson 2002). Variables in competitive models were then carried forward to a second stage where all additive combinations of these variables were generated. There was no correlation among habitat covariates ($|r| < 0.70$ for all comparisons), so multicollinearity was not an issue in the additive model stage.

This two-stage approach was repeated for each species in each year. We then evaluated the relative importance

[5] https://geodata.iowa.gov/
[6] http://ortho.gis.iastate.edu/

Table 1. Description of pond habitat variables used in breeding occupancy analyses including literature providing justification for their selection.

Variable	Description	Explanation	Justification
pH	pH of pond littoral zone, measured within quadrats along edge	pH can affect viability of eggs as well as larval development and recruitment	Pierce (1985), Freda (1986), Sparling (2010)
Slope	average slope of the pond bottom within 3 m of the shoreline	shallow littoral areas can provide habitat for foraging and refuge from predators	Adams et al. (2003), Porej and Hetherington (2005), Shulse et al. (2010)
Cattle	presence or access of cattle with direct access to the pond	cattle can trample egg masses and indirectly impact amphibians by trampling microhabitat	Trimble (1994), Trimble and Mendel (1995), Knutson et al. (2004)
log(area)	log-transformed surface area of pond	pond size can impact colonization (target effects) as well as hydrological dynamics that affect amphibian breeding use	Semlitsch and Bodie (1998), Shulse et al. (2010)
Macrophytes		wetland vegetation creates structure in the aquatic environment, providing foraging habitat and refuge from predators	Knutson et al. (2004), Shulse et al. (2010)
Emergent	average percent cover of emergent macrophytes		
Submerged	average percent cover of submerged macrophytes		
Floating	average percent cover of floating macrophytes		
Fish	presence or absence of predatory fish, including sunfish (*Lepomis* spp.), largemouth bass (*Micropterus salmoides*), and brown bullhead (*Ameiurus nebulosus*)	fish are important predators of amphibian eggs, larvae, and adults	Kats et al. (1988), Kats and Ferrer (2003)

of each variable present in stage two by calculating variable importance weights (Σw_i) by summing the AIC_c weight for all models containing that variable. We used conditional model averaging to generate real beta estimates (non-standardized), unconditional standard errors, and 85% confidence levels (after Arnold 2010) for each covariate. We generated model-averaged predicted occupancy probabilities for all habitat variables deemed biologically informative (based on their model-averaged 85% confidence levels excluding zero, after Arnold [2010]).

We used a chronosequence to determine whether important habitat variables varied by pond age class and could therefore be impacted by renovation. We generated linear regression models for five variables we expected could be linked to succession: percent cover of emergent, submerged and floating vegetation, pond slope, and pH. Vegetation and slope measurements were averaged across years for each pond (pH was measured in 2017 only). To disentangle the effect of pond age from those of other potential drivers, in addition to the explanatory variable pond age class each model also included edge woody cover and cattle presence. Models for emergent, submerged, and floating vegetation were generated with a compound Poisson (Tweedie) distribution (Tweedie 1984). Tweedie distributions can be useful for data sets containing positively skewed, zero-inflated, proportional data, like our vegetation cover data (e.g., Shulse et al. 2010). Pond slope and pH were normally distributed and were modeled with a Gaussian distribution. We then conducted a post hoc Tukey's test for pairwise comparisons to determine the presence of temporal trends based on significant differences ($\alpha = 0.05$) among age classes (after Ray et al. 2001). Chronosequence analysis was performed in R (the code used is available on Github; see *Data Availability*) with packages lsr (Navarro 2015), multcomp (Hothorn et al. 2008), and tweedie (Dunn 2017).

Results

Our surveys yielded larvae of 9 of 10 species of native pond-breeding amphibians (Appendix S1: Table S1) that have been recorded in the county (LeClere 2013), with the exception being northern leopard frog (*Lithobates pipiens*). Although our sampling was designed to target summer-breeding species, we detected tadpoles of several spring-breeding anurans including American toad (*Anaxyrus americanus*), boreal chorus frog (*Pseudacris maculata*), and spring peeper (*P. crucifer*) in ponds sampled in early June. Our detection of spring peeper represents a new vouchered county record for this species (Swartz and Miller 2016).

The farm ponds in our study exhibited a range of biotic and abiotic habitat characteristics. Cattle had access to 16 of the 51 ponds (31%). Pond ages ranged from 7 to 79 yr, with a mean estimated age of 45.2 yr (Table 2). Among the three vegetation classes, emergent vegetation

Table 2. Statistics for characteristics of study ponds located in Ringgold County, Iowa, USA, and surveyed in the summers of 2016 and 2017. With the exceptions of pond area and pond age, variables were measured at eight points around the pond.

Variable and year	Mean	Minimum	Maximum	SD
Pond age (yr)	45.20	7.00	79.00	17.76
Pond area (m^2)	1,468.13	205.02	22,299.75	4,458.51
Pond depth (cm, measured at 3 m from shoreline)				
2016	48.89	15.08	89.29	19.68
2017	48.98	15.32	93.35	17.57
Slope (rise/run)				
2016	0.13	0.02	0.36	0.07
2017	0.12	0.02	0.23	0.05
pH				
2017	8.70	6.94	10.95	1.06
Emergent vegetation cover (%)				
2016	17.13	0.00	66.25	18.50
2017	15.85	0.00	71.25	17.69
Submerged vegetation cover (%)				
2016	9.47	0.00	100.00	20.59
2017	8.30	0.00	73.13	14.71
Floating vegetation cover (%)				
2016	11.67	0.00	100.00	25.25
2017	15.74	0.00	96.88	25.24

was most prevalent. Common emergent plants included cattails (*Typha* spp.), common bur reed (*Sparganium eurycarpum*), and arrowheads (*Sagittaria* spp.). Submerged vegetation cover was dominated by common hornwort (*Ceratophyllum demersum*) and the macroalgae muskgrass (*Chara* spp.). Common floating plant species included free-floating duckweeds (*Lemna* spp.) and watermeals (*Wolffia* spp.).

Less than one-half of the ponds supported populations of predatory or non-predatory fish species. Seventeen ponds contained predatory fish (33%). Sunfish species (*Lepomis* spp.) were the most common, with green sunfish (*Lepomis cyanellus*) and bluegill sunfish (*Lepomis macrochirus*) being detected in 18% and 12% of ponds, respectively. Largemouth bass (*Micropterus salmoides*) were detected in 16% of ponds. We detected black bullhead (*Ameiurus melas*) in a single pond. Fathead minnows, which were encountered in 8% of ponds, were the only species of non-predatory fish we captured.

Detection rates and breeding occupancy

Blanchard's cricket frog, a species facing recent population declines throughout its range in the Upper Midwest (Swanson and Burdick 2010, Lehtinen and MacDonald 2011), was encountered in about one-third of ponds in each year (31.4% for 2016; 29.4% for 2017). In both years, daily detection probability for this species was moderate, but was the lowest of the species we analyzed (Table 3). The best supported explanatory variables for breeding occupancy of Blanchard's cricket frog in 2016 were submerged vegetation cover and emergent vegetation cover (Table 4). Both submerged and emergent vegetation cover were related positively to breeding occupancy probability in 2016 (Table 5). In 2017, the best-supported models were those containing either percent cover of emergent vegetation cover, pH, floating vegetation cover, or submerged vegetation cover (Table 4). However, because their model-averaged 85% confidence intervals overlapped zero, these latter three parameters from 2017 were discarded as uninformative (after Arnold 2010). This left emergent vegetation as the best explanatory variable for Blanchard's cricket frog breeding occupancy in 2017, with a positive relationship between emergent cover and occupancy probability (Fig. 3).

Gray treefrogs were observed in 27% of ponds in 2016 and 35% in 2017. In 2016, the best supported model for gray treefrog occupancy contained percent cover of emergent vegetation (Table 4). Gray treefrog occupancy was positively related to emergent vegetation cover (Table 5). The model containing pond area was also considered competitive in 2016, with gray treefrog occupancy probability related negatively to pond area. In 2017, while the models containing emergent vegetation and pond area again ranked above the null, pH, which was measured only in 2017, emerged as a better-supported explanatory variable and received all of the weight in the model set. Breeding occupancy probability of gray treefrogs was related negatively to pH (Fig. 3).

The breeding occupancy rates of plains leopard frog exhibited the most interannual variation of the species that we analyzed (Table 3). In 2016, breeding occupancy of plains leopard frog was best explained by cattle presence, littoral zone slope, emergent vegetation cover, submerged vegetation cover, and fish presence (Table 4). However, slope, submerged vegetation cover, and fish presence were subsequently discarded as uninformative (Table 5). Breeding occupancy of plains leopard frog in 2016 was positively related to cattle presence and negatively to emergent vegetation cover (Fig. 3). In 2017, the best supported variables were submerged vegetation cover and fish presence, though fish presence was again deemed uninformative. Breeding occupancy probability was related negatively to submerged vegetation cover in 2017. The effects of all variables were relatively weak in both years (Table 5) and there was substantial uncertainty around predicted occupancy for even the best-supported variables (Fig. 3).

The American bullfrog was the most common species that we encountered and it had the highest daily detection probability of the four amphibian species (Table 3).

Table 3. Year-specific mean daily detection probability along with detection covariates and naïve and adjusted breeding occupancy rates for four amphibians species captured in farm ponds (n = 51) in Ringgold County in 2016 and 2017.

Species and year	Mean daily detection probability	Detection model	Naïve occupancy rate	Adjusted occupancy rate
Blanchard's cricket frog				
2016	0.42 (0.08)	Temp + Day	0.31	0.33 (0.07)
2017	0.54 (0.08)	Day	0.29	0.31 (0.07)
Gray treefrog spp.				
2016	0.59 (0.07)	Temp	0.27	0.28 (0.06)
2017	0.62 (0.06)	Constant	0.35	0.35 (0.07)
Plains leopard frog				
2016	0.53 (0.09)	Constant	0.22	0.23 (0.06)
2017	0.60 (0.07)	Temp + Day	0.31	0.34 (0.07)
American bullfrog				
2016	0.57 (0.05)	Constant	0.69	0.70 (0.07)
2017	0.64 (0.04)	Constant	0.76	0.79 (0.06)

Notes: Mean daily detection probability was calculated by averaging the detection rate across sampling days for each species in each year. Adjusted occupancy rates were calculated from the top detection model and accounted for the influence of detection covariates, if present, on occupancy rate. Values in parentheses are SE.

Covariates included in detection models are defined as follows: Day = day of the year on which the survey took place; Temp = mean temperature on the survey day. A Constant model represents homogeneous detection across all survey days.

In both 2016 and 2017, breeding occupancy of American bullfrog was best explained by pond area (Table 4), which received the highest summed variable weight in both years (Table 5). In both years, breeding occupancy of this species was related positively to pond area (Fig. 3). Percent cover of floating vegetation also received some support in both years (Table 4), though examination of model-averaged 85% confidence intervals indicated it to be uninformative (Table 5).

Pond age and habitat development

Analysis of the pond chronosequence indicated that pond age class, cattle presence, and shoreline tree cover each influenced some habitat characteristics (see Appendix S1: Table S2). Shoreline tree cover had a significant effect on emergent vegetation (P = 0.041), floating vegetation (P = 0.032), and pond slope (P = 0.048). Cattle presence was found to have significant effect on floating vegetation (P = 0.033) and pond slope (P = 0.030). Tukey's tests indicated that there were significant differences among pond age classes for pH and pond slope (Appendix S1: Table S3), with both being lower in ponds older than the renovation threshold age (≥40 yr old; Fig. 4e, d). While differences in emergent vegetation among age classes were not statistically significant, average percent cover trended higher in older ponds and only one pond younger than 40 yr old had > 20% emergent vegetation cover (Fig. 4a). Neither floating nor submerged vegetation cover differed significantly among pond age classes.

Discussion

The two goals of this study were to identify the species-specific habitat components that make farm ponds suitable for amphibians and to explore the potential impact of pond renovation on habitat availability by examining the timing of habitat development. It is clear from our results that farm ponds in southern Iowa provide breeding habitat for amphibian populations. Our findings support previous work that found practices such as elimination of wetland vegetation to be likely detrimental to some amphibian species (Porej and Hetherington 2005, Shulse et al. 2010). Given the influence of succession on habitat quality, we have found that pond renovation is an unrecognized threat to amphibian habitat. Our work highlights the challenges of balancing ecological and agricultural functions of sites when conserving wildlife in working agricultural landscapes.

Farm ponds are designed to serve critical agricultural functions in the landscapes of the central U.S. Our results suggest that management of ponds to maintain these functions will favor certain amphibian species and disadvantage others. For example, the American bullfrog, the most common species in our study, is known to tolerate a wide range of habitat conditions (Casper and Hendricks 2005). We found that American bullfrog exhibited a strong preference for larger ponds, but otherwise showed little association with other habitat conditions. This may be due to the fact that larger ponds are more likely to maintain high water levels and thus provide suitable overwintering habitat for bullfrog larvae (Casper and Hendricks 2005). Pond management driven by the sole goal of maintaining high agricultural functioning (permanent water) will likely favor this common amphibian species.

In contrast, two species of conservation concern, gray treefrogs and Blanchard's cricket frog, both bred in ponds with habitat conditions more characteristic of unmanaged, late-stage succession. In both years, Blanchard's cricket frog and gray treefrogs showed strong associations with high levels of emergent vegetation. Our chronosequence analyses demonstrated that these emergent vegetation conditions developed almost exclusively in older ponds (>40 yr), though they did not always

TABLE 4. Analysis of single season occupancy models using the Akaike information criterion corrected for sample size (AIC_c) for four species of amphibians from farm ponds in Ringgold County in the summers of 2016 and 2017.

Species and model	K	ΔAIC_c	w_i	Deviance
Blanchard's cricket frog 2016				
Submerged	5	0.00	0.61	−57.70
Emergent	5	2.25	0.20	−58.83
Null	4	4.72	0.06	−61.30
Blanchard's cricket frog 2017				
Emergent	4	0.00	0.79	−54.18
pH	4	5.41	0.85	−56.89
Floating	4	5.51	0.90	−56.94
Submerged	4	6.59	0.93	−57.48
Null	3	6.60	0.96	−58.66
Gray treefrog spp. 2016				
Emergent	4	0.00	0.91	−55.82
log(area)	4	5.68	0.05	−58.66
Fish	4	7.83	0.02	−59.73
Floating	4	9.51	0.01	−60.57
Submerged	4	10.01	0.01	−60.82
Null	3	10.79	0.00	−62.39
Gray treefrog spp. 2017				
pH	3	0.00	1.00	−57.96
Emergent	3	18.66	0.00	−67.29
log(area)	3	22.94	0.00	−69.43
Fish	3	24.26	0.00	−70.09
Slope	3	25.95	0.00	−70.94
Null	2	32.06	0.00	−75.12
Plains leopard frog 2016				
Cattle	3	0.00	0.69	−49.95
Slope	3	4.10	0.09	−52.00
Emergent	3	5.06	0.06	−52.49
Fish	3	5.08	0.05	−52.49
Submerged	3	5.38	0.05	−52.65
Null	2	6.00	0.03	−54.09
Plains leopard frog 2017				
Submerged	5	0.00	0.74	−60.53
Fish	5	4.75	0.07	−62.91
Null	4	5.22	0.05	−64.37
American bullfrog 2016				
log(area)	3	0.00	0.45	−117.11
Floating	3	2.02	0.16	−118.12
Null	2	2.12	0.16	−119.30
American bullfrog 2017				
log(area)	3	0.00	0.82	−117.71
Floating	3	5.68	0.05	−120.55
Null	2	6.14	0.04	−121.91

Note: The null (detection-only) model and all models ranked higher than it are presented. Models presented by species and by year (2016 or 2017, year denoted with subscript). Variables are w_i, Akaike weight, interpreted as the probability that the given model is the best-approximating model of the candidate set, and K, the number of estimable parameters in the model, including the intercept.

occur. Unfortunately, while favorable to certain amphibians, these conditions are perceived to hinder agricultural function. Limiting or eliminating wetland vegetation, often considered to be "weedy," has long been a hallmark of farm pond management (Compton 1952, Leja 1998). The apparent importance of emergent vegetation cover for breeding habitat of these species suggests a need to reconsider how pond vegetation management affects wildlife.

Another key habitat component associated with gray treefrog breeding was pond pH. Treefrogs bred almost exclusively in ponds with a circumneutral pH (7–8). Selection of these sites may reflect the deleterious effect of extreme pH levels on sperm motility, egg hatch rate, and larval development (Sparling 2010). The association of gray treefrogs with circumneutral pH conditions raises an important conflict between agricultural and conservation functions. Suitable conditions for gray treefrogs developed only in the two oldest pond age classes (50–59 and 60+ years old). If older ponds are renovated when they begin to suffer from decreased agricultural function, suitable gray treefrog breeding sites would be entirely absent from the landscape.

Cattle and fish, while sometimes considered to be the key factors limiting the conservation value of farm ponds for amphibians (Leja 1998), did not feature prominently in our results. Plains leopard frog breeding occupancy probability for ponds where cattle were present was nearly double that of ponds without cattle. However, this effect was only evident in 2016. In 2017, plains leopard frogs occupied an additional five ponds, including several where cattle were absent, and support for cattle's influence diminished substantially. These results suggest that the relationship between plains leopard frog breeding occupancy and cattle presence is at best weak. Other habitat variables also exhibited inconsistency among years. For example, submerged vegetation cover was a well-supported explanatory variable for Blanchard's cricket frog occupancy in 2016, but it received little support in 2017. This variation may be due to a combination of the size of our sample of ponds and variation in occupancy rates among years. Thus, variables for which the yearly results are inconsistent should be interpreted with caution. Relationships that were well-supported in both years, like emergent vegetation cover for Blanchard's cricket frog or pond area for American bullfrog, can be interpreted with greater confidence.

It is unclear why there was no evidence for a negative relationship between breeding occupancy and cattle presence in this study, though it may be due in part to the low stocking rate of cattle in our system. Study ponds were located on pastures grazed at reduced stocking rates (2.5 animal unit months/ha; Duchardt et al. 2016) to facilitate grassland restoration (Miller et al. 2012, Duchardt et al. 2016). At these low stocking rates, cattle presence may not result in the severe negative impacts reported in other studies. However, we cannot verify this hypothesis since an experimental comparison of the effects of high and low stocking rate was not performed in this study and other comparable farm pond studies, such as Knutson et al. (2004), do not report

Table 5. Model-averaged real parameter estimates (β), unconditional standard errors (SE), and lower and upper 85% confidence intervals (after Arnold 2010) for habitat variables associated with breeding occupancy of four amphibian species in 2016 and 2017 (year denoted in subscript following species name).

Species and parameter	Σw_i	β	SE	85% confidence interval Lower	Upper
Blanchard's cricket frog 2016					
Submerged	0.99	0.07	0.03	0.02	0.11
Emergent	0.97	0.06	0.02	0.03	0.09
Blanchard's cricket frog 2017					
Emergent	0.90	0.06	0.02	0.02	0.09
Floating	0.47	0.02	0.02	0.00	0.04
Submerged	0.40	0.03	0.03	−0.01	0.07
pH	0.35	−0.46	0.44	−1.1	0.18
Gray treefrog spp. 2016					
Emergent	0.99	0.07	0.02	0.04	0.10
log(area)	0.84	−2.57	1.21	−4.31	−0.84
Gray treefrog spp. 2017					
pH	1.00	−4.45	1.52	−6.64	−2.26
Plains leopard frog 2016					
Cattle	0.83	2.09	0.94	0.73	3.45
Emergent	0.72	−0.06	0.04	−0.12	−0.01
Fish	0.52	−1.87	1.3	−3.74	0.01
Slope	0.40	−11.02	9.68	−24.96	2.92
Submerged	0.35	−0.04	0.05	−0.11	0.03
Plains leopard frog 2017					
Submerged	0.90	−0.12	0.07	−0.21	−0.02
Fish	0.37	−0.93	0.8	−2.07	0.22
American bullfrog 2016					
log(area)	0.70	1.96	1.17	0.28	3.63
Floating	0.44	−0.02	0.02	−0.04	0.00
American bullfrog 2017					
log(area)	0.96	3.46	1.38	1.48	5.45
Floating	0.55	−0.03	0.02	−0.05	0.00

Note: Σw_i is the summed Akaike weight for models in which variable is present; it indicates relative variable importance.

stocking rates. Furthermore, we did not assess whether amphibian larvae in our study sites were experiencing any of the sublethal or indirect effects associated with the presence of cattle (Schmutzer et al. 2008).

Similarly, the lack of notable responses of our focal species to fish presence does not necessarily indicate that stocking fish does not pose a risk to the broader amphibian community. There is evidence that the species we studied may be less affected by fish invasion than other members of the community (Lannoo 1998). The effects of fish on more vulnerable species may still be substantial.

While our results raise the possibility that livestock watering and amphibian conservation could be compatible in situations where cattle can be grazed at low stocking rates, the negative impacts of cattle grazing on amphibians and wetlands are well documented in other contexts (e.g., Knutson et al. 2004, Schmutzer et al. 2008). The broader literature makes clear that cattle and fish tend to degrade amphibian habitats, not improve them, and both should be excluded from farm ponds if amphibian conservation is the primary goal (Knutson et al. 2004, Giuliano 2006).

The trade-offs involved in balancing amphibian conservation with agricultural function of farm ponds underscore the potential importance of a landscape perspective on pond conservation, sometimes referred to as a "pondscape" approach (Sayer et al. 2012). While each pond may offer suitable habitat for a subset of the regional species pool, it is unlikely, and unnecessary, for every site to support all species (Boothby and Hull 1997, Hassall et al. 2012). A functional pondscape thus contains a heterogeneous collection of ponds, together representing a suite of habitat types and successional states.

The issue of renovation highlights the need for a pondscape approach. As ponds enter later successional stages, their agricultural function declines (Renwick et al. 2006, Chumchal and Drenner 2015). We found that this process is paralleled by an increase in the capacity of ponds to provide suitable breeding habitat for species like gray treefrogs and Blanchard's cricket frog. Renovating ponds will lead to a short-term loss of habitat for these species. Although they may still return to and attempt to reproduce in recently renovated ponds (see Pechmann et al. 2001), their reproductive success will likely be low due to a lack of suitable habitat. In contrast, the newly renovated ponds might still be suitable for the American bullfrog and other generalists returning to ponds post-renovation. Future study of how site fidelity and colonization behavior affect amphibian use and breeding success in renovated ponds could provide valuable insights into the immediate effects of renovation on amphibian behavior and reproductive success.

In any case, our results suggest that retaining older ponds in their late-successional state should be a priority for conserving amphibians in these landscapes. However, the proliferation of late-successional ponds conflicts with efforts to protect against drought, a key concern for farmers in the region (Coon et al. 2018). Reconciling these conflicting goals requires an approach that acknowledges the challenges of conserving habitat in working agricultural landscapes. The pondscape framework is particularly appealing for this reason. Maximizing both agricultural function and habitat conservation in a single pond is unnecessary, and likely impossible, but both goals could be met at a landscape scale by maintaining a mosaic of pond successional states. Ponds on productive cattle pastures or in erosion-prone drainages could be maintained in early successional states whereas ponds less critical to the farm enterprise could

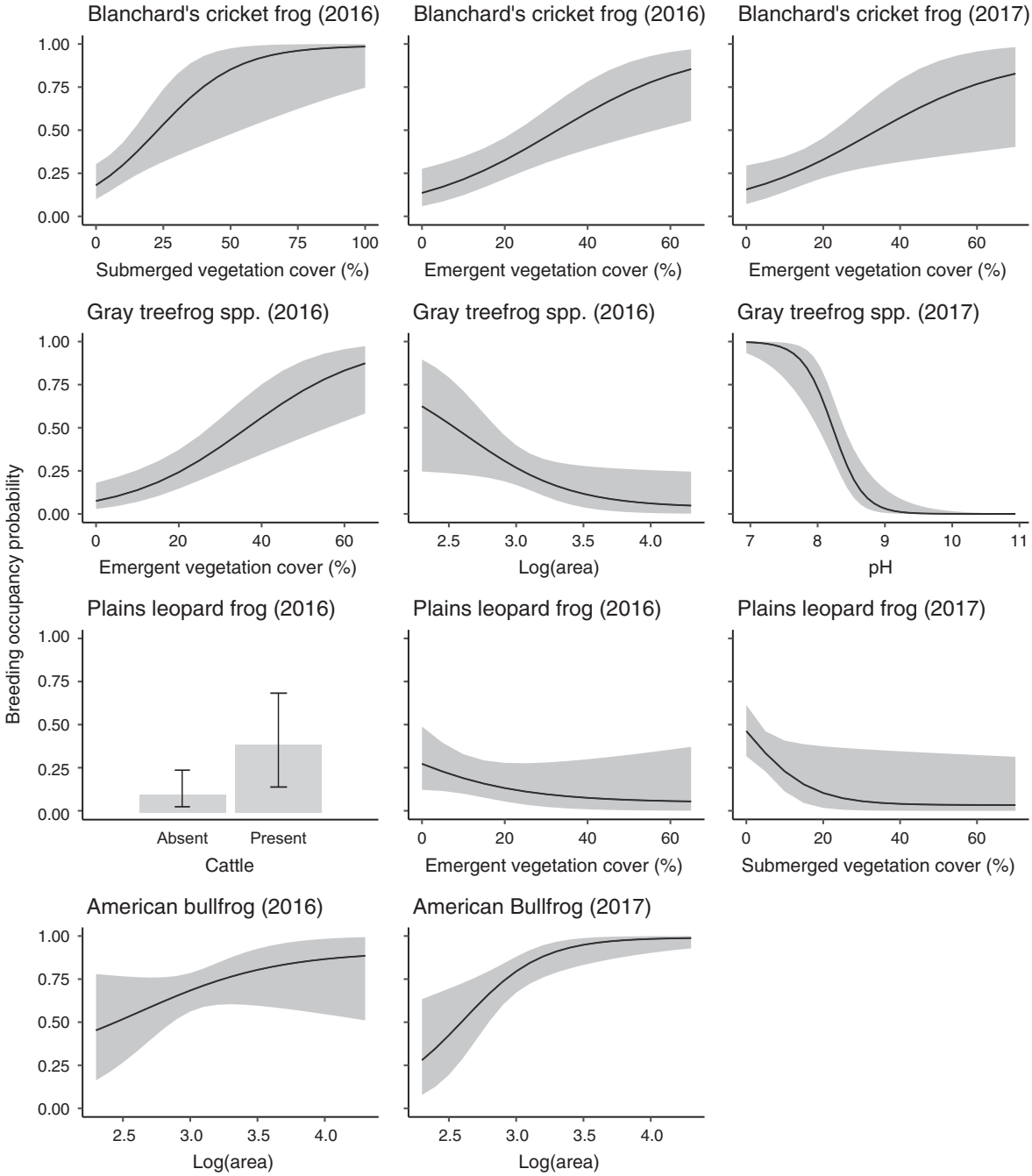

FIG. 3. Model-averaged predicted breeding occupancy probability and 85% confidence intervals for four species of pond-breeding amphibians. Plots shown for the best-supported habitat variables in each year (i.e., those variables that were deemed biologically informative, see *Methods*). In some years, more than one variable was informative for a species. Occupancy probability was predicted across the range of the variable. Other variables, if present, were held at their means. See Table 1 for habitat variable descriptions. Data collected in summers of 2016 and 2017 in Ringgold County, Iowa.

be reserved as amphibian habitat and permitted to reach later successional conditions.

A pondscape approach would represent a major change from current practices in the United States. Today, farm ponds are excluded from wetland protections under the Clean Water Act (Clean Water Act 1972) and their integration into regional amphibian conservation strategies remains challenging due to their anthropogenic nature (Kingsbury and Gibson 2012). For a road map for implementing this approach, we may

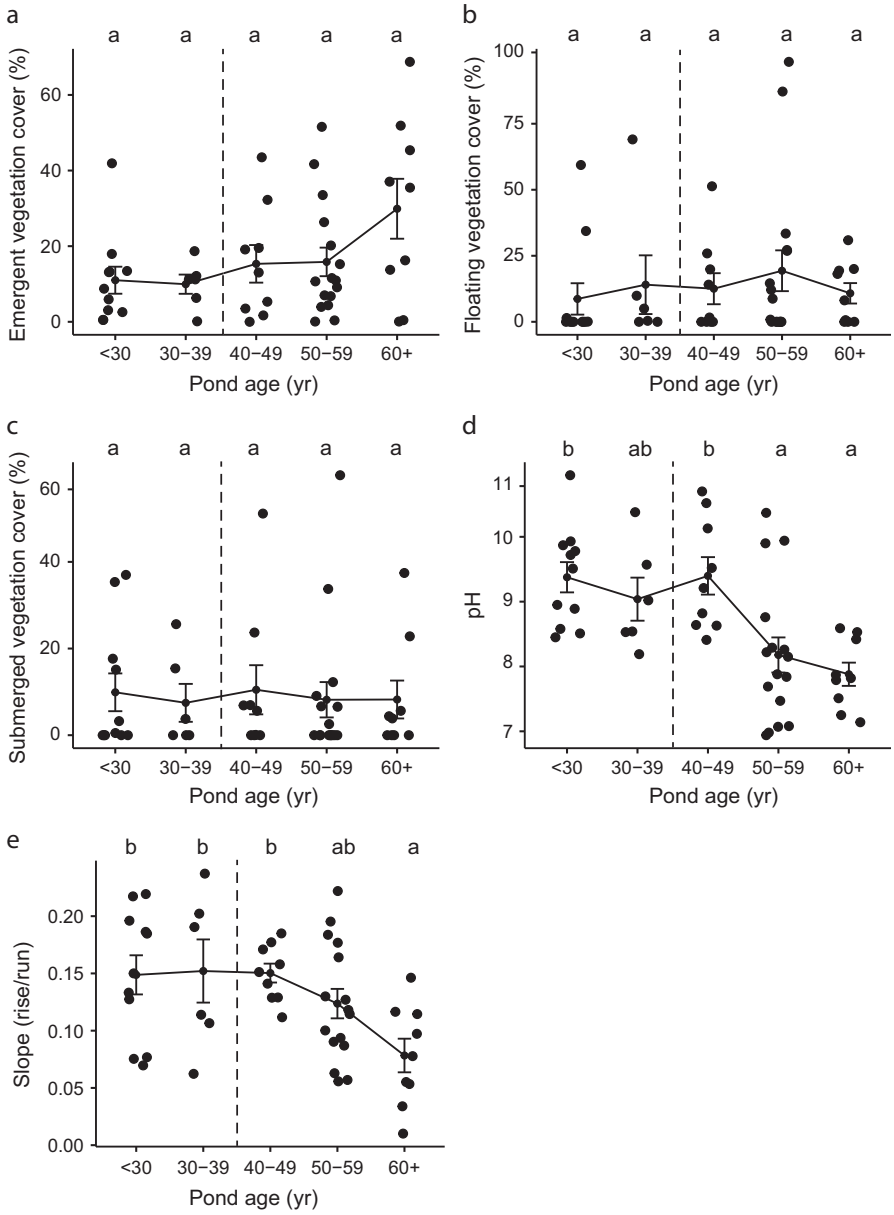

FIG. 4. Mean values for emergent vegetation cover (a), floating vegetation cover (b), submerged vegetation cover (c), pH (d), and slope (e) by pond age class. Error bars represent standard error. Different letters denote significant differences among groups using Tukey's method for pairwise comparisons. Significance was determined based on an alpha level of 0.05. It should be noted that, while there were no significant differences among age classes for emergent vegetation (a), very few young ponds (<40 yr old) contained high levels of emergent vegetation cover (>25%). Dashed line denotes the renovation threshold or the age (~40 yr) after which renovation is typically used to restore agricultural function. See Table 1 for habitat variable descriptions. Data collected in June and July of 2016 and 2017 in Ringgold County, Iowa.

look to pond conservation initiatives in Europe. At Manor Farm in Norfolk, UK, pondscape heterogeneity is maintained by periodic removal of sediments and overgrown vegetation, ensuring that sufficient numbers of early- and mid-successional habitats are present (Sayer et al. 2012). Similarly, in many agricultural regions of Japan (see Toyama and Akasaka 2017) and Europe (see Curado et al. 2011 and Hartel and von Wehrden 2013), ponds have fallen into disuse due to rural land abandonment, and management would focus on preventing dominance of late-successional ponds. On the other hand, in regions like our study area where farm ponds are relatively recent additions to the landscape, early-successional ponds likely predominate. In these areas, pondscape management would focus on allowing ponds to mature despite the decrease in agricultural

function that accompanies habitat development. Regardless of context, the goal would be to maintain a pondscape comprised of sites at various stages of succession to maximize its capacity to support biodiversity.

The Conservation Reserve Program (CRP) could provide a template for a policy mechanism for promoting pondscape management. The CRP provides incentives for landowners to take agricultural lands out of production and reserve them as wildlife habitat for up to 30 yr. As part of the program, landowners are required to perform mid-contract management activities focused on managing the successional state of the site (for example, Matthews et al. 2012). A similar approach to incentivize a succession-based management program for farm ponds could yield considerable benefits for biodiversity conservation.

As the most pond-rich region of the United States, the Great Plains holds substantial potential for conservation of aquatic flora and fauna, including amphibians. However, there are also challenges to reconciling biodiversity conservation with the agricultural uses of farm ponds. Our study provides information about amphibian use of farm ponds in this region, but also raises several important questions about the outlook for their conservation. This study is the first to acknowledge and describe the threat that pond renovation could pose to amphibian communities in U.S. farm ponds, but a wider assessment of both its social drivers and ecological outcomes is also needed. Ultimately, the attitudes and behavior of landowners define the quality and availability of amphibian habitat on private lands, and understanding the extent to which landowners are willing to adopt new management strategies to conserve amphibians in their ponds remains a critical research goal.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1964/full

Data Availability

Data are available through Figshare: https://doi.org/10.6084/m9.figshare.8258795.v1. R code are available through Zenodo: https://doi.org/10.5281/zenodo.3243628