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RESEARCH ARTICLE

A Quantitative Assessment of the Conservation Benefits of the Wetlands Reserve Program to Amphibians

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Abstract

The Mississippi Alluvial Valley (MAV) originally consisted of nearly contiguous bottomland hardwood (BLH) forest encompassing approximately 10 million hectares. Currently, only 20–25% of the historical BLH forests remain in small patches fragmented by agricultural lands. The Wetlands Reserve Program (WRP) was established to restore and protect the functions and values of wetlands in agricultural landscapes. To assess the potential benefit of WRP restoration to amphibians, we surveyed 30 randomly selected WRP sites and 20 nearby agricultural sites in the Mississippi Delta. We made repeat visits to each site from May to August 2008 and performed both visual encounter and vocalization surveys. We analyzed the encounter history data for 11 anuran species using a Bayesian hierarchical occupancy model that estimated detection probability and probability of occurrence simultaneously for each species. Nine of the 11 species had higher probabilities of occurrence at WRP sites compared to agriculture. Derived estimates of species richness were also higher for WRP sites. Five anuran species were significantly more likely to occur in WRP than in agriculture, four of which were among the most aquatic species. It appears that the restoration of a more permanent hydrology at the WRP sites may be the primary reason for this result. Although amphibians represent only one group of wildlife species, they are useful for evaluating restoration benefits for wildlife because of their intermediate trophic position. The methods used in this study to evaluate the benefit of restoration could be used in other locations and with other groups of indicator species.

Key words: **anuran, delta, detection probability, hierarchical model, Mississippi, occupancy, species richness**

Introduction

Extending from southern Illinois to the mouth of the Mississippi River in Louisiana, the lower Mississippi Alluvial Valley (MAV) historically contained nearly contiguous bottomland hardwood (BLH) forest wetlands over an estimated 10 million hectares (Putnam et al. 1960; Hefner & Brown 1985; King et al. 2006). However, after a major flood in 1927, extensive levee development and channelization altered the hydrology of the MAV, reducing, or even eliminating new wetland formation in many areas of the MAV (Fredrickson 2005; King et al. 2005, 2006). Upon elimination of the threat of flooding in the MAV, BLH forests on these fertile alluvial soils were quickly converted to agriculture (Twedt & Best 2004) and by the 1940s only 50% of the native forests remained (Twedt & Loesch 1999). Today, only 20–25% of the forest in the MAV remains, and these are most often small and highly fragmented patches, separated from each other by nonforest land cover, usually agriculture (Rudis 1995; Twedt & Loesch 1999; King et al. 2006). Conversion to agricultural production accounts for an estimated 96% of BLH forest losses in the MAV (MacDonald et al. 1979).

In an attempt to restore and protect the functions and services of wetlands in agricultural landscapes, the Wetlands Reserve Program (WRP) was established in the 1990 Farm Bill and reauthorized in the 1996, 2002, and 2008 Farm Bills, respectively. Administered by the USDA Natural Resources Conservation Service (NRCS), the WRP is a voluntary program providing landowners financial incentives and technical assistance to restore wetlands on their property, usually on lands that would otherwise function as marginal farmland (King et al. 2006). These marginal areas are typically in lower landscape positions where ditches and other drainage measures have not succeeded well enough for viable farming. Restoring riparian wetland hydrology in the MAV is typically complicated and expensive resulting in limited extent or effectiveness (King et al. 2006; Hunter et al. 2008). Although one objective of the WRP is to restore habitat for wetland-dependent wildlife, there have been few quantitative studies measuring the benefit to wildlife species of WRP conservation practices

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(Gray & Teels 2006). In a recent review, Faulkner et al. (2011) found no studies specific to the MAV; however, results from other regions of the country have reported positive effects from wetland restoration on amphibian abundance and species richness (Vasconcelos & Calhoun 2006; Milne & Bennett 2007; Petranka et al. 2007). This knowledge gap is especially important to amphibians because wetland hydrology is a critical component of their habitat.

Amphibians, especially anurans, are ideal model organisms to determine restoration success in this landscape for several reasons: (1) anurans use agricultural habitats, thus could colonize WRP sites (Knutson et al. 2004); (2) anurans rely on suitable hydrology for reproduction (Vasconcelos and Calhoun 2006; Liner et al. 2008); (3) anurans exhibit rapid colonization of new suitable habitats (Lehtinen & Galatowitsch 2001; Pechmann et al. 2001); and (4) anurans can comprise a significant proportion of biomass in wetlands with important implications in food web linkages as both predator and prey (Gibbons et al. 2006). Therefore amphibians are expected to colonize and increase in abundance if restoration is successful. In addition, amphibians have experienced worldwide declines, with a major factor in the observed declines and extinctions being habitat loss (Johnson 1992; Green 1997; Alford & Richards 1999; Lannoo 2005; Gallant et al. 2007). Thus, any habitat restored and suitable for amphibian persistence will aid in thwarting any future declines in the MAV.

Here we investigate anuran occupancy at selected WRP and agricultural sites in the MAV to determine the magnitude of benefit from WRP restoration for amphibians. Our objectives were to estimate the proportion of restored and agricultural sites occupied for each anuran species detected and estimate total anuran species richness at each site. We used a multispecies Bayesian hierarchical formulation of a single-season occupancy model to produce estimates by land use type for comparison. We expected that both anuran occupancy and species richness would be greater at WRP sites compared to agricultural sites.

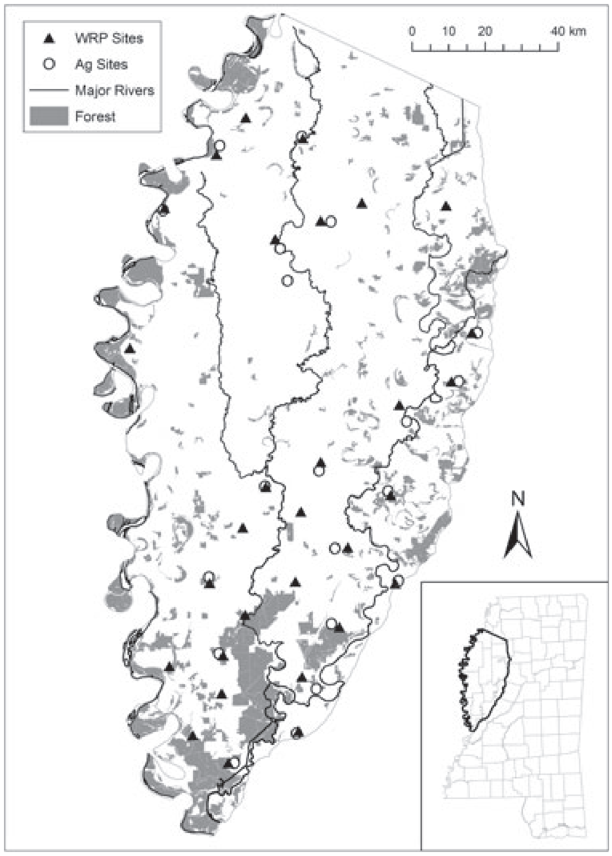

Figure 1. Map of the study area in Mississippi consisting primarily of the Mississippi Delta portion of the Yazoo River Basin. WRP and agricultural study sites are indicated along with the remnant tracts >1 km^2 of bottomland hardwood forest (2006 National Land Cover Database).

Methods

Study Sites

This study was conducted within the Mississippi Delta portion of the Yazoo River Basin, a 16,000 km^2 area that lies within 15 counties in northwest Mississippi, USA (Fig. 1). The original vegetation in the region was primarily BLH forest, but the vast majority of BLH has been converted to agricultural use (2006 National Land Cover Database). Currently, only about 3,340 km^2 of BLH still exists in the region, and most of that is found on wildlife refuges and small, isolated tracts ($\bar{x} = 8.1$ ha, $s = 113.5$ ha; Fig. 1). As of 2005, 325 sites have been enrolled in the WRP in this area, accounting for 37,866 ha (NRCS unpublished data). Most of these WRP sites have been planted with typical BLH tree species and have undergone some type of hydrological restoration.

We selected WRP sites from the study area at random using a GIS data layer obtained from the NRCS, but only tracts of sufficient size (>40 ha) that had been enrolled in the WRP program for at least 6 years were included in the study. To reduce bias due to spatial autocorrelation, all selected WRP sites were at least 5 km from the nearest other selected WRP site. A total of 52 sites were originally selected using these criteria, but 22 of these sites were rejected due to difficulty obtaining landowner permission, difficult access, or because WRP enrollment was too recent. The 30 selected WRP tracts were 47–503 ha ($\bar{x} = 200$ ha) in size. For comparison with the sampled WRP sites, an additional 20 agricultural sites ($\bar{x} = 81$ ha) were selected in close proximity to WRP sites (<5 km distant). Usually, agricultural sites were adjacent or nearly adjacent to the WRP sites and were under the same ownership as the WRP. All of the agricultural sites were partially cultivated in crops, but each contained some area of field edge or drainage ditch that held sufficient ponded water to harbor anurans during the study period. Standing water usually covered a smaller area at agricultural sites and was thus more ephemeral than the water at the WRP restoration sites.

Field Sampling

We used two complementary techniques to sample for anurans at each site: visual encounter surveys and vocalization surveys.

Sampling effort was concentrated on the portions of the WRP or agricultural site deemed most likely to harbor amphibians, and the same location within each site was sampled during the repeat visits. The sampling location was generally around the most permanent water at the site; usually a water control structure at a WRP or a drainage ditch at an agricultural site. Sampling was conducted at night beginning no sooner than 30 minutes after sunset, and sampling on any given night was usually concluded by 0100 hours. Each visual encounter survey was time constrained to last one person hour and was performed by 2–3 experienced observers using high-power head lamps. Observers sampled in such a way as to maximize the number of species detected as opposed to the number of individuals of any one species detected by searching in a variety of microhabitats. We made an effort to capture each individual amphibian encountered to positively identify the species and measure the snout-to-vent length (mm). During the concomitant vocalization survey, all anurans heard calling within an estimated 100 m of the sampling location were noted. We excluded vocalizations heard from outside of this radius as it was impossible to determine if they represented individuals calling from the same land use category as the study plot.

Each of the 50 study sites was sampled on three separate nights between 5 May and 4 August 2008. The mean time to complete all three surveys of a site was 17 days (range 3–28 days), an interval we believe short enough to meet the assumption that sites were closed to changes in occupancy by species. During each sample, we measured air temperature and relative humidity with a portable weather meter (Kestrel 3000, Nielsen Kellerman, Boothwyn, PA, U.S.A.).

Data Analysis

We used a hierarchical formulation of a multispecies occupancy model to estimate the probabilities of detection and occurrence of each anuran species and to derive an estimate of species richness at each plot (Kéry & Royle 2008; Royle & Dorazio 2008). In this community level occupancy model each species has its own detection probability, occurrence, and treatment response. Binomial detection and nondetection data ($1 =$ present, $0 =$ not detected) of $i = 1, 2, \ldots, N$ species during $j = 1, 2, \ldots, J$ samples of $k = 1, 2, \ldots, K$ sites are input in the form of an array y_{ijk}. Note that species are known to occur at the site with certainty if detected, but as in standard occupancy models (Mackenzie et al. 2006) nondetection of a species does not necessarily mean the species does not occur at the site. Although similar models have been described that use data augmentation methods to estimate occurrence of species not detected during the sampling (cf. Kéry & Royle 2008), we have chosen to use a model without hypothetical unobserved species as this is not likely to be useful information for managers interested in evaluating the restoration benefits of WRP (Russell et al. 2009; Urban & Swihart 2011).

The occurrence of a species at a site is denoted z_{ik}, where $z_{ik} = 1$ if species i is present at site k and is 0 if otherwise. The y_{ijk} are assumed to be Bernoulli random variables if the species is present, but take the value $y_{ijk} = 0$ with probability 1 if the species does not occur at the site (i.e. $z_{ik} = 0$). Thus, whether a species is observed at a sample of a site is conditional on the occurrence state variable z,

$$y_{ijk} \sim \text{Bern}(p_{ijk} z_{ik}) \tag{1}$$

where p_{ijk} is the probability that a species is detected during a sample of a site. Likewise, z is a latent variable that is assumed to be distributed Bernoulli on the probability of occurrence of the species at the site, ψ_{ik}:

$$z_{ik} \sim \text{Bern}(\psi_{ik}). \tag{2}$$

This model assumes that heterogeneity in p and ψ among species takes a normal distribution such that each species may have a unique value. In addition, covariates for both detection and occurrence may be incorporated into the model using a logit transformation. We considered environmental parameters collected during each survey to be important detection covariates. The values for temperature and humidity were standardized so that the means were zero, and the logit transform of detection probability was modeled as:

$$\text{logit}(p_{ijk}) = \alpha_0 + \alpha_1 \text{ AirTemp} + \alpha_2 \text{ Humidity} \tag{3}$$

We used the land use category of each site as a covariate for occurrence. Agricultural sites were modeled as the baseline and the effect of a land use being WRP relative to agriculture was modeled as:

$$\text{logit}(\psi_{ik}) = \beta_0 + \beta_1 \text{WRP} \tag{4}$$

We estimated the model parameters and derived summaries from our hierarchical model using Bayesian analysis methods (Royle & Dorazio 2008). We used vague priors distributed uniform from 0 to 1 for community level detection and occurrence, and distributed normal with mean zero and variance = 100 for habitat and detection effects. This model was fit using Markov chain Monte Carlo (MCMC) methods in Program WinBUGS (Spiegelhalter et al. 2003). We used three parallel MCMC chains of 120,000 in length, discarding the first 20,000 of each as burn-in with a thinning rate of 10. Convergence was assessed based on the R-hat potential scale reduction values of each parameter (Gelman & Hill 2007). All estimates of parameters are reported as medians and 95% Bayesian credible intervals of the posterior.

Results

During the visual encounter surveys, we observed 1051 anurans of 11 different species (Table 1). The majority of captures were made at WRP sites, but directly comparing counts is inappropriate because it fails to account for heterogeneity in detection probability and because more WRP sites than agriculture sites were sampled. No species was heard vocalizing

Table 1. Count of anurans observed during visual encounter surveys at the 20 agricultural sites and 30 WRP sites.

Species	*Agriculture*	*WRP*
American Bullfrog *Lithobates catesbeianus*	13	108
American Toad *Anaxyrus americanus*	1	0
Green Frog *Lithobates clamitans*	4	19
Cope's Gray Treefrog *Hyla chrysoscelis*	1	3
Eastern Narrow-mouthed Toad *Gastrophryne carolinensis*	4	5
Fowler's Toad *Anaxyrus fowleri*	86	28
Green Treefrog *Hyla cinerea*	39	192
Northern Cricket Frog *Acris crepitans*	14	160
Pickerel Frog *Lithobates palustris*	2	9
Southern Leopard Frog *Lithobates sphenocephalus*	102	260
Spring Peeper *Pseudacris crucifer*	0	1
Total	266	785

in this study that was not also detected in the course of visual encounter surveys. For this reason, we feel that it is unlikely that including vocalization data in our analysis caused our model to violate the assumption that sites are closed to changes in occupancy (MacKenzie et al. 2002).

Estimated detection probabilities (p) varied widely among species and in relation to air temperature and relative humidity. Detection probability generally increased with increasing air temperature (observed range 16–31°C) and with increasing humidity (observed range 54–99%), but one species (Cope's Gray Treefrog) displayed the inverse relationship with temperature and some species showed little effect of temperature or humidity on detection. Three species (American Toad, Pickerel Frog, and Spring Peeper) had average detection probabilities that were below 0.30, a level below which estimates of occurrence are often biased (MacKenzie et al. 2002). These species were also among the least encountered of this study (Table 1).

Minimum occupancy, defined as the proportion of sampled sites where a species was detected on at least one occasion, varied from 0.0 to 0.85 for the 11 anuran species among agriculture sites (Table 2). Posterior estimates of probability of occurrence (ψ) for each species in agriculture ranged from 0.073 to 0.854, indicating that all species had some probability of occurring in agriculture (Table 2). Minimum occupancy among WRP sites ranged from 0.0 to 1.0 for the 11 anuran species (Table 3), and estimates of ψ were between 0.241 and 0.992. Estimates of the WRP effect β parameter (Equation 4) were positive for all 11 anuran species (Fig. 2), indicating a higher probability of occurrence at a WRP relative to an agriculture site. The 95% credible interval includes 0 for six of the species (Fig. 2), which could be interpreted as a lack of statistical significance at the $\alpha = 0.05$ level. For five of the six most commonly encountered species (Table 1), however, the effect of WRP relative to agriculture was significant (Fig. 2). Fowler's Toad was the only frequently encountered species ($n = 114$) that did not have a significant WRP effect.

The total species richness of anurans across all agriculture and WRP sites was similar, with all 11 species having some probability of occurrence in both land use types. The mean of the derived estimates of anuran richness at agriculture sites was four species, whereas the mean estimate of richness at the WRP sites was eight (Fig. 3). Four agriculture sites had a higher species richness comparable to that of the WRP sites (Fig. 3), but these sites differed from the other agriculture sites in that they were cultivated in rice which involves managing fields to flood for extended periods.

Discussion

Our results demonstrate that WRP restoration projects in the Mississippi Delta provide a measurable benefit to anuran amphibians by increasing the probability of occurrence of species and the species richness of the anuran community

Table 2. Summary of occurrence modeling for agricultural sites in the study area.

Common name	*Minimum occupancy*	*ψ (SD)*	*Lower 95% CI*	*Upper 95% CI*
American Bullfrog	0.40	0.419 (0.103)	0.229	0.629
American Toad	0.05	0.226 (0.303)	0.007	0.967
Bronze Frog	0.25	0.264 (0.094)	0.115	0.480
Cope's Gray Treefrog	0.05	0.073 (0.066)	0.013	0.254
Eastern Narrow-mouthed Toad	0.15	0.218 (0.162)	0.058	0.705
Fowler's Toad	0.65	0.668 (0.117)	0.438	0.896
Green Treefrog	0.45	0.477 (0.105)	0.276	0.681
Northern Cricket Frog	0.35	0.393 (0.103)	0.203	0.604
Pickerel Frog	0.10	0.306 (0.273)	0.037	0.964
Southern Leopard Frog	0.85	0.854 (0.082)	0.659	0.971
Spring Peeper	0.00	0.133 (0.272)	0.002	0.929

Minimum occupancy is the proportion of sampled agricultural sites at which the species was observed, and ψ is the estimated probability of occurrence of each species in agriculture (median of posterior sample) along with the 95% Bayesian credible interval (CI).

Table 3. Summary of occurrence modeling for WRP sites in the study area.

Common name	*Minimum occupancy*	ψ *(SD)*	*Lower 95% CI*	*Upper 95% CI*
American Bullfrog	0.87	0.893 (0.061)	0.749	0.987
American Toad	0.00	0.272 (0.400)	0.002	0.999
Bronze Frog	0.63	0.692 (0.094)	0.503	0.868
Cope's Gray Treefrog	0.20	0.241 (0.103)	0.103	0.487
Eastern Narrow-mouthed Toad	0.27	0.466 (0.212)	0.206	0.987
Fowler's Toad	0.73	0.859 (0.092)	0.653	0.995
Green Treefrog	0.97	0.954 (0.039)	0.850	0.996
Northern Cricket Frog	0.97	0.953 (0.043)	0.839	0.998
Pickerel Frog	0.10	0.551 (0.330)	0.079	0.999
Southern Leopard Frog	1.00	0.992 (0.017)	0.940	1.000
Spring Peeper	0.03	0.406 (0.372)	0.011	0.998

Minimum occupancy is the proportion of sampled WRP sites at which the species was observed, and ψ is the estimated probability of occurrence of each species in WRP (median of posterior sample) along with the 95% credible interval (CI).

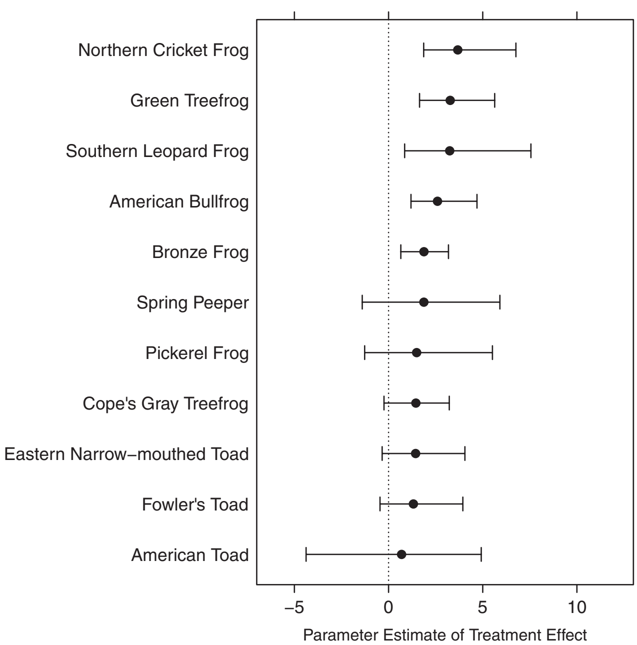

Figure 2. Estimates with 95% credible interval of the logit-scale β for the effect of land use at a site being WRP relative to agriculture on the probability of occurrence (ψ) of each species. Values greater than 0 are considered positive (e.g. the species is more likely to occur at WRP sites) and estimates with 95% credible intervals that include 0 are not considered statistically significant.

at WRP sites relative to agriculture sites. Estimates of ψ were greater in WRP sites than agriculture sites for 9 of the 11 anuran species in this study, but it should be noted that all species had at least some probability of occurrence in agriculture. This illustrates the important point that all of the anuran species found in this study can occur in the predominant agricultural habitat. This is significant because it suggests that a source for colonization of anurans already exists in the land adjacent to the WRP restorations (Knutson et al. 2004; Rannap et al. 2009; Lesbarrères et al. 2010). Although various anurans are able to persist in an agricultural landscape, WRP sites promote higher site occupancy and, thus, a higher species

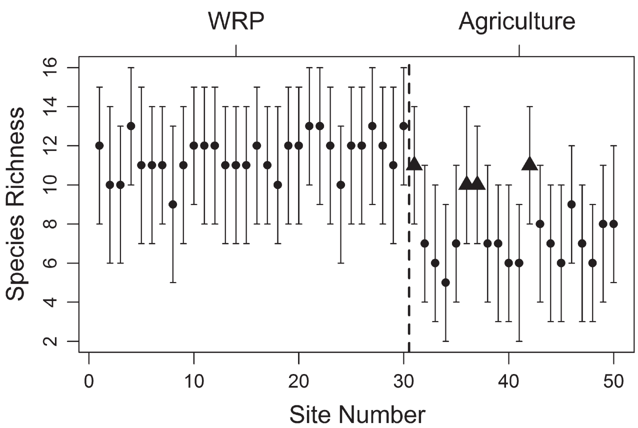

Figure 3. The median value and 95% credible interval from the posterior estimates of species richness of anurans at each site separated by land use. The four agricultural sites indicated with triangles rather than circles were sites where the fields were flooded for the production of rice as opposed to standard cultivated fields.

richness. This result confirms that WRP restorations provide a benefit to wildlife relative to agriculture.

Although we have no direct measurements of the hydrology at the study sites, the value of the WRP restoration for amphibians appears to be primarily due to the hydrologic restoration of the sites. All the WRP sites in our study had some sort of permanent or nearly permanent impounded water that could be managed with control structures (King et al. 2006). Four of the five species that were significantly more likely to occur in WRP than in agriculture are considered highly aquatic (Northern Cricket Frog, Southern Leopard Frog, American Bullfrog, and Bronze Frog). These four species generally inhabit areas with permanent water (Mount 1975; Dundee & Rossman 1989) and are therefore most likely to benefit from the restored hydrology of WRP. An exception that proves this point is the four agricultural sites we sampled that were planted in rice with flooded field. These sites had species richness similar to that of WRP, including the highly aquatic species. Rice cultivation in other areas has been shown to support high richness of amphibian species (Machado & Maltchik 2010; McIntyre et al. 2011). Anuran species with shorter larval periods appear to find suitable breeding sites at both WRP and agricultural sites. Although restoration of bottomland forest will be beneficial for many species, it seems that the most immediate benefit for many anurans is in restoration of wetland hydrology.

Fowler's Toad was one species that we encountered a disproportionately large number of times at agricultural sites. Both Fowler's Toad and the American Toad had higher estimates of occurrence in agriculture than at WRP sites, although the effect of WRP was not significant for either species. The toad species have a high tolerance for dry conditions and prefer sandy soils (Brown 1974; Green 2005) like the ones found adjacent to fields and ditches in the study area. In addition, they breed in shallow temporary water that is free of fish that are predators of their larvae. Therefore, Fowler's and American Toads are not likely to show a preference for WRP sites over agriculture, and our model results demonstrate this.

Amphibians are highly suitable as indicators of successful restoration of wetland habitat in this system because they are easily sampled with a few visits per site during the appropriate time of year (Gagné & Fahrig 2007). The occupancy modeling technique we employed using the Bayesian hierarchical model is especially efficient because it allows the estimation of occurrence of all species, even the seldom encountered ones and provides an estimate of species richness while accounting for imperfect detection (Kéry & Royle 2008). In addition to the economic reasons to use amphibians as indicators of restoration success, it is likely that amphibians are responding to changes in the habitat that benefit other species as well. Amphibians are predators of invertebrates and some small vertebrates like fish. Other vertebrates, especially birds, also rely on this prey base and on amphibians themselves as prey. Therefore, the trophic position of amphibians in this system along with the cost-effective sampling techniques make amphibians excellent indicators of the benefit of WRP to wildlife.

Although we assert that the visual encounter and vocalization methods used in this study are appropriate for sampling a broad range of anurans, there are important caveats for using these data. Counts of individuals reported here should not be used as an index of abundance. This is true primarily because counts unadjusted for varying detection probability are potentially misleading (Williams et al. 2002), but also because there was uneven sampling between agriculture ($n = 20$ sites) and WRP ($n = 30$ sites). Detection probability varied with temperature and humidity for some, but not all species, and not necessarily in the same direction. Some of the species in the study area, especially the Spring Peeper and the Southern Leopard Frog, tend to breed prior to our initial sampling date. Thus, our sampling likely missed the annual peak in detectability for these species. Because the occupancy model we used estimates detection probability and occurrence simultaneously, we account for the uncertainty in the observation process when estimating occupancy (Mackenzie et al. 2006; Royle & Dorazio 2008). Our study was not intended to identify specific WRP conservation practices responsible for improving the site for amphibians, but rather to determine if restoring marginal cropland through the WRP was beneficial to these taxa.

There are several possible reasons why WRP sites could have higher rates of occupancy and higher species richness of anurans than agricultural sites in the Mississippi Delta. The water control structures used in the hydrologic restoration of the WRP sites produce a more favorable hydrology than what is found in typical agricultural ditches of the region (King et al. 2006). The presence of more natural vegetation around the edge of the WRP wetlands is also more beneficial (Knutson et al. 2004). Water quality (turbidity, presence of pesticides, etc.) may also be improved at WRP sites compared to agriculture. However, the most important benefit of the WRP lands for amphibians may be the long-term (>30 yr) conservation easements that protect the habitat into the future.

Implications for Practice

- With conservation easements >30 years, the Wetlands Reserve Program (WRP) provides a long-term means to encourage habitat and hydrologic restoration of bottomland hardwood forests, which have been reduced by nearly 80% in the Mississippi Alluvial Valley.
- Anurans living in the predominately agricultural landscape provide a source of colonizing species to WRP areas when hydrologic and habitat restoration has occurred.
- The statistical approach applied in this study provides a method to estimate species richness of the anuran community while accounting for imperfect detection of individuals.
- Amphibians are a highly suitable and cost-effective indicator of WRP restoration success that can be easily sampled with repeat site visits during the appropriate time of year.

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