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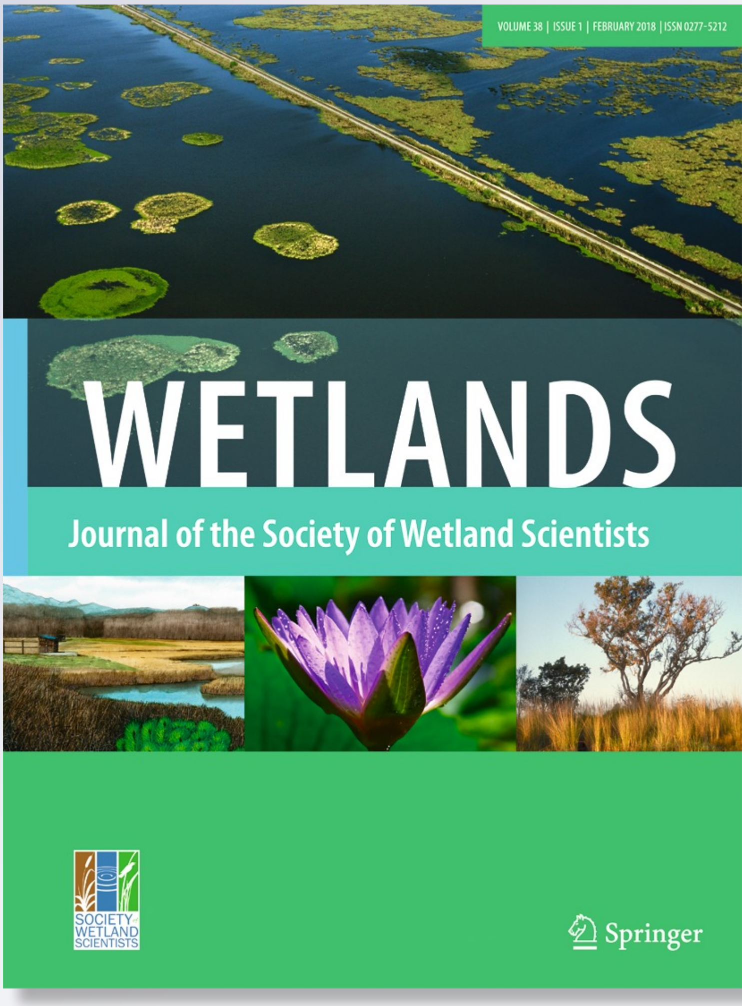

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ORIGINAL RESEARCH

Herpetofaunal Communities in Restored and Unrestored Remnant Tallgrass Prairie and Associated Wetlands in Northwest Arkansas, USA

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Abstract Wetlands within tallgrass prairie are among the most endangered ecosystems in North America and serve as critical habitat for many sensitive and endemic species. Although loss of these habitats has acutely affected reptiles and amphibians, most prairie restoration initiatives take an ecosystem restoration approach adapted for plant and/or game species, with few focusing particularly on herpetofauna. Limited information exists documenting the population responses of reptiles and amphibians to wetland restoration in tallgrass prairie ecosystems. We used multiple techniques to compare reptile and amphibian communities in recently (2006) restored and unrestored tallgrass prairie and associated wetland habitats at Woolsey Wet Prairie Sanctuary (WWPS), a wetland mitigation site in Northwest Arkansas (USA). We documented 24 reptile and amphibian species and found that *Regina grahamii* (Graham's Crayfish Snake) and *Lithobates areolatus* (Crawfish Frog), both of which are considered species of greatest conservation need in the state, showed preferential use of restored habitat, while common, widespread species did not use restored or unrestored habitat preferentially. Our results demonstrate that restoration of tallgrass prairie and associated wetlands benefits rare and sensitive herpetofauna and highlight two important management considerations: 1) promoting ephemeral (fishless) hydrology, and 2) emphasizing terrestrial movement corridors and critical upland habitat.

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Introduction

Prairie and associated wetland ecosystems support a great diversity of taxa (Risser 1988; Euliss et al. 1999), including many specialist species, and often contain high levels of endemism (Knopf 1996). In North America, these biodiverse ecosystems have experienced widespread destruction due to extirpation of native grazers, introduction of exotic vegetation, conversion of land to agriculture, and fire suppression (Warner 1994; McLaughlin and Mineau 1995; Twidwell et al. 2013). Prior to European colonization, approximately 162 million ha of prairie existed throughout the Great Plains region (Samson and Knopf 1994). However, North American tallgrass prairies and associated wetlands are now the most imperiled ecosystems world-wide (The Nature Conservancy 2016).

Wetlands are vital components of many grassland ecosystems (Bolen et al. 1989; Eldridge 1990; Mushet et al. 2002; Euliss et al. 2004). Hydrologic and thermal variation in wetlands generate heterogeneous soils (Richardson et al. 2001), vegetative coenoclines (Seabloom et al. 1998), and diverse habitat structure (Murkin et al. 1997), which promote biological diversity (Weller 1982). However, the fertile, hydric soils of prairie-associated wetlands make them desirable for crop or livestock production. Conversion of these wetlands for agricultural purposes results in alterations to the natural hydrology (van der Kamp et al. 1999) and disruption of native plant communities (Matson et al. 1997), often to the extreme of creating irrigated monocultures (Liu et al. 2004). Pervasive agricultural techniques explain why today, less than 50% of historic wetlands remain world-wide (Dahl 1990).

In the last century, efforts to restore degraded prairie and associated wetlands have increased substantially in the Great Plains region of the United Sates. The goal of prairie and wetland restoration is often to restore ecological integrity to degraded habitat and maximize ecosystem services (e.g., flood mitigation, nutrient sequestration, and wildlife production; Zedler and Kercher 2005). In the context of prairie and wetland restoration, landscapes must be liberated from the structural uniformity typical of degraded prairie, and provided with natural landscape features such as topographic relief, seasonal inundation, and diverse vegetative structure and composition (Biebighauser 2011). Restoration usually begins with the removal of over-dominant or exotic plant species, which is necessary for successful propagation of native prairie grasses (Gould and Gorchov 2000), followed by prescribed burning to limit ecological succession and encroachment of woody vegetation (Gibson and Hulbert 1987).

Plants are often the focal taxa in the restoration of prairies and their associated wetlands (Streever 1999), with animals presumed to colonize from surrounding habitats thereafter (Zedler 2000). This assumption may be flawed because restoration efforts are often applied within fragmented landscapes that have been isolated from remnant historical habitat (Lehtinen et al. 1999; McCoy and Mushinsky 1999). Critically fragmented landscapes may feature corridors which allow passive transport of plant propagules (Damschen et al. 2008), but restrict or prevent colonization by animals with low vagility or acute physiological sensitivity to environmental conditions, such as amphibians and reptiles (Joly et al. 2003; Scherer et al. 2012).

Amphibians and reptiles (herpetofauna) comprise a substantial component of vertebrate diversity and biomass in prairie-associated wetland ecosystems (Iverson 1982; Deutschman and Peterka 1988; Hecnar and M'Closkey 1997; Gibbons et al. 2006), but are currently experiencing unprecedented population declines at a global scale (Alford et al. 2001; Gibbons et al. 2000; Stuart et al. 2004). The cryptic behavior and unpredictable activity patterns of reptiles and amphibians generally confer low detectability (Durso et al. 2011; Willson et al. 2011); therefore, the population status or even regional distribution of many species are still poorly known (Todd et al. 2010). While some studies have examined herpetofaunal communities in fire-maintained forests and grasslands (e.g. Wilgers and Horne 2006; Perry et al. 2009), less is known about their responses to restoration of tallgrass prairie and associated wetlands.

Our objective was to compare herpetofaunal communities of recently-restored remnant tallgrass prairie and associated wetlands in Northwest Arkansas, USA, to those of neighboring unrestored habitats that are currently degraded by agriculture and non-native vegetation cover. We hypothesized that: 1) reptile and amphibian species richness and relative abundance would be greater in restored habitats and 2) relative abundances in restored habitats would reflect stronger responses by species that, within our region, are generally associated with remnant tallgrass prairie habitat and associated wetlands, such as *Regina grahamii* (Graham's Crayfish Snake; Fowler 2015) and *Lithobates areolatus* (Crawfish Frog; Parris and Redmer 2005).

Methods

Study Site

Woolsey Wet Prairie Sanctuary (Fig. 1) contains a 16.6-ha mitigation site constructed to offset the permanent loss of 3.6 ha of adjacent wetlands associated with a wastewater system improvement project within the Osage Prairie region (Washington County, Arkansas, USA). This region is characterized by the climatic (Brye et al. 2004), topographic (King et al. 2002), and edaphic (Chapman and Horn 1967) transition from the arid Great Plains region of Oklahoma and Kansas to the humid-temperate, deciduous plateaus of the Ozark Highlands in Arkansas and Missouri. Nearly all historic prairie in this region has experienced moderate to severe degradation from agriculture and/or urbanization, but observable prairie mound (Nebkha) microtypography suggests that much of WWPS (restored and unrestored) has not been extensively tilled in the past. Restoration of WWPS was designed to restore ecosystem features of native tallgrass prairie including seasonal inundation and periodic drying. To achieve these hydrologic modifications, earthen berms were constructed and equipped with water control structures. Following wetland construction in 2006, selective herbicide treatments were applied to control invasive plants and prescribed burns were performed annually each spring. Vegetation in upland portions of the site is dominated by weedy native species including *Panicum anceps*, *Tridens flavus*, *Andropogon virginicus*, *Setaria parviflora*, *Solidago altissima*, *Eupatorium serotinum*, and *Vernonia missurica*, scattered with more conservative prairie species such as *Baptisia alba*, *Helianthus mollis*, *Penstemon digitalis*, *Pycnanthemum pilosum*, *P. tenuifolium*, *Asclepias hirtella*, *A. viridis*, *Orbexilum pedunculatum*, and *Rosa carolina*. Swales and lower areas are dominated by a diverse assemblage of sedges (*Carex* spp., *Cyperus* spp., *Eleocharis* spp., *Scirpus* spp., and *Rhynchospora* spp.) and rushes (*Juncus* spp.), mixed with *Andropogon hirsutior*, *Tridens strictus*, *Paspalum floridanum*, several forbs including *Eupatorium perfoliatum*, *Boltonia asteroids, B. diffusa*, *Persicaria* spp., and several woody species including *Cephalanthus occidentalis*, *Salix nigra*, and *Fraxinus pennsylvanica*.

Restored units within WWPS ("West and Center Unit" and "East Unit") are comprised of a mix of seasonal depressional wetlands and upland grasslands, resulting in a gradient of

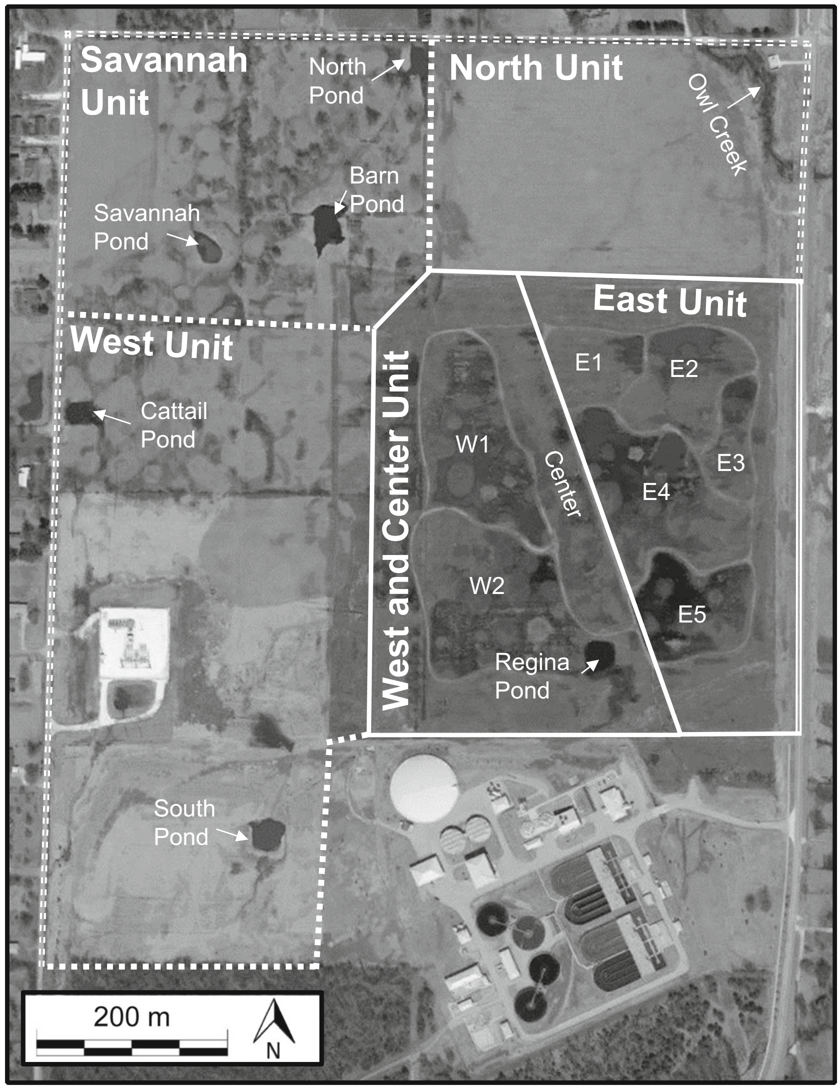

Fig. 1 Aerial photograph of study site: Woolsey Wet Prairie Sanctuary (WWPS), Northwest Arkansas, USA. Restored prairie units (West and Center, and East Unit) are contained within solid lines and unrestored units (West, North, and Savanna Unit) are contained within dashed lines. Habitat regions bordered by roads are denoted with doubled solid and dashed lines. Unit names are denoted in bold typeface, and sub-units or aquatic habitats are denoted in non-bold typeface

wetland size and permanence (Fig. 1). Most wetland areas are seasonal and all dry during extreme droughts; no fish were detected in any wetlands at the site during the study period. The vegetative coenocline reflects patterns in soil moisture from dry, upland soils, to transitional, seasonally saturated soils at the wetland-upland interface. Isolated *Salix* spp. (Willow) stands exist in wetlands with comparatively long hydroperiods and the site is bordered by deciduous forest on its southern boundary (Fig. 1). Natural upland habitat features are sparse throughout WWPS, with little downed woody debris or rock. Unrestored units of WWPS ("North Unit," "Savannah Unit," and "West Unit"; 33.8 ha) that surround the restoration zone are primarily maintained as hay fields dominated by non-native *Lolium arundinaceum* (Tall Fescue) and represent areas slated for future restoration. In the North Unit and southern portions of the West Unit, microtopographic variation (prairie mounds) is reduced (Fig. 1), likely due to shifts in soil composition and possibly historic tilling. Five discrete fishless artificial farm ponds with relatively long (semi-permanent) hydroperiods are found in the unrestored regions (Fig. 1). Emergent vegetation is limited in the North and South Pond and is dominated by *Typha* sp. (Cattail) in the West Pond.

Given the small size of our study area, we recognize that movement of animals among wetlands or habitat units was possible (and was likely for some species). Likewise, the limited number of replicated sites (wetlands or units) within each habitat category precluded a formal analysis to quantify detection and occupancy probabilities (MacKenzie and Royle 2005). Thus, recognizing that species detection probability was imperfect (<1), we caution that non-detections do not imply species absence (Pellet and Schmidt 2005), and focus our analyses instead on relative abundance (see below) as an indicator of habitat use, rather than focusing primarily on species richness.

Reptile and Amphibian Sampling

Anuran Call Surveys We conducted anuran call surveys at four restored wetlands (E2, E4/E5 [combined due to proximity], Regina Pond, and W1; Fig. 1) and five unrestored wetlands (North Pond, Barn Pond, Savanna Pond, Cattail Pond, and South Pond; Fig. 1) once per week from early spring (15 March) to mid-summer (10 July) 2014. To maximize detectability and ensure uniform survey conditions, we conducted call surveys between 2100 and 2400 h (Williams et al. 2012b; Williams et al. 2013) on nights with weather conducive for amphibian breeding activity (mild temperatures, high humidity, and low wind-speed), and if possible, following rain events. For each survey, 1–2 observers listened independently for 5 min at each wetland unit, recording all species heard. Maximum calling intensity over the 5 min period for each anuran species was ranked based on a numeric call index defined by the North American Amphibian Monitoring Program (0 = silent, no audible calls; 1 = individuals can be counted, there is space between calls; 2 = calls of individuals can be distinguished, but there is some overlapping of calls; 3 = full chorus, calls are constant, continuous and overlapping; Weir and Mossman 2005). At the end of the 5 min survey, the observers conferred and determined a consensus call intensity for each species; given the broad categories used, there was seldom disagreement between observers.

Aquatic Trapping We used commercially available plastic minnow-traps (Gator Buckets; model: 700) to passively assess the occurrence of aquatic reptiles and amphibians within wetlands (Keck 1994; Willson et al. 2008). To compare relative abundances of aquatic snakes and larval amphibians among restored and unrestored wetlands, we performed systematic trapping one week each month between March and June 2014, with ten traps set in each of 11 wetlands (restored: E2, E4, E5, Center, Regina Pond, and W1; unrestored: North Pond, Barn Pond, Savanna Pond, Cattail Pond, and South Pond; Fig. 1). Crayfish were also captured using this technique, and were counted along with aquatic snakes and larval amphibians. Traps were spaced approximately 2 m apart and partially submerged in shallow vegetated habitats, with 5–6 cm of headspace inside the trap to ensure animals had access to air. We checked all traps daily, and identified, counted, and immediately released amphibians during the first 2–3 days each month (larval amphibians and small crayfish captured after this period were retained in the traps to serve as bait for snakes). We identified all adult anurans to species; however, because *L. areolatus* and *L. sphenocephalus* are nearly indistinguishable in the field (Trauth et al. 2004), *Lithobates* larvae (which accounted for >90% of minnow trap captures) were only identified to genus. Once captured, we transported all snakes to the laboratory to measure their mass and body length. We then marked snakes individually using a disposable medical cautery unit (Winne et al. 2006), and returned them to their approximate capture location within seven days. Although wetlands began to dry after June, trapping was continued later in the summer to assess seasonal activity of aquatic species. In July, four of the original 11 semi-permanent wetlands held water and were trapped (restored: Regina Pond, E4; unrestored: Barn Pond, Savanna Pond), for a total of 700 trap-nights, with equal effort in restored and unrestored habitats. In September and October, Barn Pond dried; therefore, we trapped the three remaining wetlands for a total of 684 trap-nights.

Time-Constrained, Visual Encounter & Coverboard Surveys We performed time-constrained visual encounter surveys (VES) weekly from 18 February 2014 to 25 June 2014. The entire site was divided into five units (restored: East and West/Center [combined due to size and proximity]; unrestored: North, Savannah, and West; Fig. 1). During VES, each unit was surveyed for 30 min by 1–10 observers, with equal effort per unit. Observers opportunistically searched visually under natural cover for reptiles and amphibians. Particular emphasis was placed on terrestrial habitats, because these were underrepresented by other methods. We deployed plywood coverboards (1.5 cm X 70 cm X 80 cm) on 11 March 2014 to serve as artificial cover objects (restored: $N = 35$; unrestored: $N = 35$; Grant et al. 1992; Willson and Gibbons 2009) and check during VES surveys. Additionally, we performed weekly coverboard checks from 4 July to 6 November. We conducted visual surveys and coverboard checks at mid-day in spring and fall, and at night during the summer.

Analyses

We compared use of restored and unrestored habitats using relative abundance indices (i.e., counts standardized for effort, or anuran call indices). These methods may not detect all individuals (i.e., detection probabilities are <1); thus, counts may underestimate true abundance (Schmidt and Pellet 2010). A key assumption when using counts as indices of abundance is that detection probabilities are similar among statistical units. Without empirical detection probability estimates (Schmidt 2003), we attempted to minimize variation in detection probability due to observer bias, environmental conditions, and sampling effort. Specifically, we conducted each anuran call survey during a short temporal window (<2 h; ensuring similar environmental conditions) with the same observers, trapped all sites simultaneously (ensuring similar environmental conditions), standardized minnow trap counts for effort, and marked snakes to avoid re-counting individuals. However future efforts to rigorously compare abundance or population size among habitats would benefit from a mark-recapture framework incorporating estimates of individual detection probability in abundance estimation.

Anuran Calls To compare anuran call intensity among wetlands, we only considered calls recorded during peak breeding season for each species. We categorized species by breeding seasons based on temporal call modalities; early spring breeders (15 March – 8 April): *L. areolatus* (Crawfish Frog), *Pseudacris crucifer* (Spring Peeper), *Pseudacris fouquettei* (Cajun Chorus Frog), *Lithobates sphenocephalus* (Southern

Leopard Frog), *Anaxyrus americanus* (American Toad); late spring breeders (20 April – 5 June): *Hyla versicolor* (Gray Treefrog), *Acris blanchardi* (Blanchard's Cricket Frog); summer breeders (11 June – 10 July): *Lithobates catesbeianus* (American Bullfrog). *Gastrophryne carolinensis* (Eastern Narrowmouth Toad) were sparsely recorded, and thus were not included in the analysis. For each species, we compared mean intensities among restored ($N = 4$) and unrestored ($N = 5$) wetland units using *t*-tests, with wetland as the statistical unit and $\alpha = 0.05$. Because of violations of assumptions of normality and/or homoscedasticity, we analyzed data for *L. areolatus*, *L. catesbeianus*, *P. crucifer*, *P. fouquettei*, and *A. americanus* using Mann-Whitney *U* tests.

Aquatic Trapping To compare relative abundances of larval *Lithobates* sp. and crayfish among wetland types, we restricted analyses to the first 2–3 days (when all trap contents were counted and emptied daily) of each monthly trapping period between March and June (when equal effort was used at restored and unrestored wetlands). We standardized captures for effort by dividing daily capture totals by the number of traps deployed. Standardized counts (captures per trap-night) were then averaged within each wetland and compared among restored ($N = 6$) and unrestored ($N = 5$) wetland units. Because of unequal variances between tadpole abundance and non-normal distribution of crayfish in restored wetlands, we used Mann-Whitney *U* tests to compare these groups and a *t*-test to compare *A. texanum* larvae, with wetland as the statistical unit and $\alpha = 0.05$. We summed snake captures over the March – June trapping period and excluded recaptures of individuals within wetlands to avoid confounding assessments of aquatic snake relative abundances by differences in recapture probability among habitats. We compared total numbers of individual *R. grahamii* and *Nerodia erythrogaster* (Plain-bellied Watersnake) captured per wetland among restored ($N = 6$) and unrestored ($N = 5$) wetland units using *t*-tests. Other snake species were not captured frequently enough in aquatic traps to warrant statistical comparisons. We performed all analyses in the R statistical programming environment (v. 3.4.1; R Core Team 2017).

Time-Constrained, Visual Encounter & Coverboard Surveys We compiled the total captures of snakes from systematic visual encounter and coverboard surveys. Although low numbers of captures precluded statistical evaluation of these patterns, we cautiously interpret differences in total captures, given that sampling effort was equal in restored and unrestored units.

Results

We observed a total of 24 amphibian and reptile species during this study (nine anurans, one salamander, three turtles, one lizard, ten snakes); 21 and 24 species were detected in the restored and unrestored section, respectively (Table 1). Visual Encounter Surveys detected the greatest number of species ($N = 20$) and documented several species not detected using other methods: *Plestiodon fasciatus* (Common Five-lined Skink), *Chelydra serpentina* (Common Snapping Turtle), *Trachemys scripta* (Red-eared Slider), and *Terrapene carolina* (Eastern Box Turtle). Aquatic trapping yielded the greatest number of captures of all methods, particularly for amphibian larvae ($N = 134$ *A. texanum* and $N = 14{,}154$ Ranid tadpoles) and aquatic snakes. Coverboards were the most effective method for detecting terrestrial snakes (Table 1), especially *Thamnophis proximus* (Western Ribbonsnake). Auditory Call Surveys detected all anuran species recorded during the study, including one species, *Anaxyrus americanus*, which was not detected by other methods.

Anurans

During anuran call surveys, *H. versicolor*, *A. blanchardi, P. crucifer*, *P. fouquettei*, and *L. sphenocephalus* were detected at all wetlands, regardless of restoration status, while the remaining anuran species were detected at only a subset of the wetlands. *Anaxyrus americanus* used three of four restored and four of five unrestored wetlands. *Gastrophryne carolinensis* were detected only in four of five unrestored wetlands (although *G. carolinensis* were detected in restored wetlands with coverboards and minnow traps; Table 1). *Lithobates areolatus* used all restored and two of five unrestored wetlands, while *L. catesbeianus* used one of four restored and one of five unrestored wetlands. The mean number of anuran species detected did not differ substantially among restored and unrestored wetlands (restored = 7.0, unrestored = 7.2).

The largest difference in calling intensity was seen in *L. areolatus*, which had an eight-fold higher mean calling intensity in restored wetlands than in unrestored wetlands (Mann-Whitney *U* test, $U_{1,7} = 19.5$, $p = 0.024$; Fig. 2). *Pseudacris fouquettei* also exhibited significantly greater call intensity in restored wetlands ($U_{1,9} = 20$, $p = 0.016$). Conversely, *P. crucifer* tended to have greater call intensities in unrestored areas ($U_{1,7} = 2$, $p = 0.062$). Calling intensities of *A. americanus*, *L. sphenocephalus*, *H.versicolor*, *A. blanchardi*, and *L. catesbeianus* did not differ significantly between restored and unrestored wetlands (all $p > 0.05$).

Aquatic Trapping

Aquatic traps yielded a total of 301 snake captures of 111 individual *R. grahamii* and 39 individual *N. erythrogaster*. *Nerodia sipedon* and *T. proximus* were seldom captured in traps ($N = 8$ and 5 individuals, respectively). Excluding recaptures, relative abundance of *R. grahamii* was almost five-fold greater in restored wetlands than in unrestored wetlands (*t*-test, $t = -2.59$, d.f. = 5.68, $p = 0.044$), but relative abundance of *N. erythrogaster* did not vary significantly between habitats

Table 1 Total captures of herpetofauna at Woolsey Wet Prairie, Arkansas, USA, in 2014 by species, location, and detection method. Mean calling intensities are indicated parenthetically for anuran species. Calling intensity of each anuran species was ranked based on a discrete numeric call index (0–3) and average values for each unit listed parenthetically beside capture total

Class	Order	Species	Restored		Unrestored			Method of detection	Total captures
			East	West and Center	West	Savannah	North		
Amphibia	Anura	*Lithobates* sp. (larvae)	8110	4192	173	1679	0	MT	14,154
		Lithobates sphenocephalus	176 (1.27)	204 (1.20)	21 (0.80)	321 (0.90)	4 (1.40)	MT, VES, AC	726
		Acris blanchardi	8 (1.25)	15 (0.88)	23 (1.94)	20 (1.50)	7 (2.63)	MT, VES, AC	73
		Lithobates catesbeianus	26 (0.20)	11 (0.00)	3 (0.00)	9 (0.10)	3 (0.00)	MT, VES, AC	52
		Pseudacris fouquettei	24 (2.67)	5 (2.80)	5 (1.40)	17 (1.90)	† (1.80)	MT, CB, VES, AC	51
		Pseudacris crucifer	† (1.13)	† (1.60)	† (1.90)	9 (2.50)	† (2.40)	MT, VES, AC	9
		Lithobates areolatus	4 (1.40)	† (2.20)	. (0.00)	4 (0.50)	. (0.00)	MT, AC	8
		Gastrophryne carolinensis	2 (0.00)	. (0.00)	† (0.50)	† (1.30)	5 (1.00)	MT, CB, AC	7
		Anaxyrus americanus	† (0.53)	† (1.80)	† (0.20)	† (0.20)	† (0.00)	AC	.
		Hyla versicolor	† (1.00)	1 (1.13)	† (0.81)	† (1.25)	2 (2.13)	MT, VES, AC	3
	Caudata	*Ambystoma texanum*	47	84	157	236	.	MT, CB	524
Reptilia	Squamata	*Nerodia erythrogaster*	49	52	2	68	5	MT, CB, VES	176
		Regina grahamii	35	111	3	19	.	MT, CB, VES	168
		Thamnophis proximus	31	44	11	55	1	MT, CB, VES	142
		Thamnophis sirtalis	3	7	5	19	5	CB, VES	39
		Lampropeltis calligaster	2	2	3	5	2	CB, VES	14
		Nerodia sipedon	.	.	2	6	6	MT, VES	14
		Coluber constrictor	.	2	6	3	.	CB, VES	11
		Pantherophis obsoletus	.	.	5	3	.	CB, VES	8
		Lampropeltis holbrooki	.	1	3	.	.	CB, VES	4
		Storeria dekayii	1	.	.	2	.	CB, VES	3
		Plestiodon fasciatus	.	.	.	3	.	VES	3
	Testudines	*Chelydra serpentina*	2	7	1	3	.	VES	13
		Trachemys scripta	5	2	3	1	.	VES	11
		Terrapene carolina	1	4	1	.	.	VES	6

MT, minnow trapping; *VES*, visual encounter survey; *AC*, anuran call survey; *CB*, coverboard survey, † = only detected auditorily

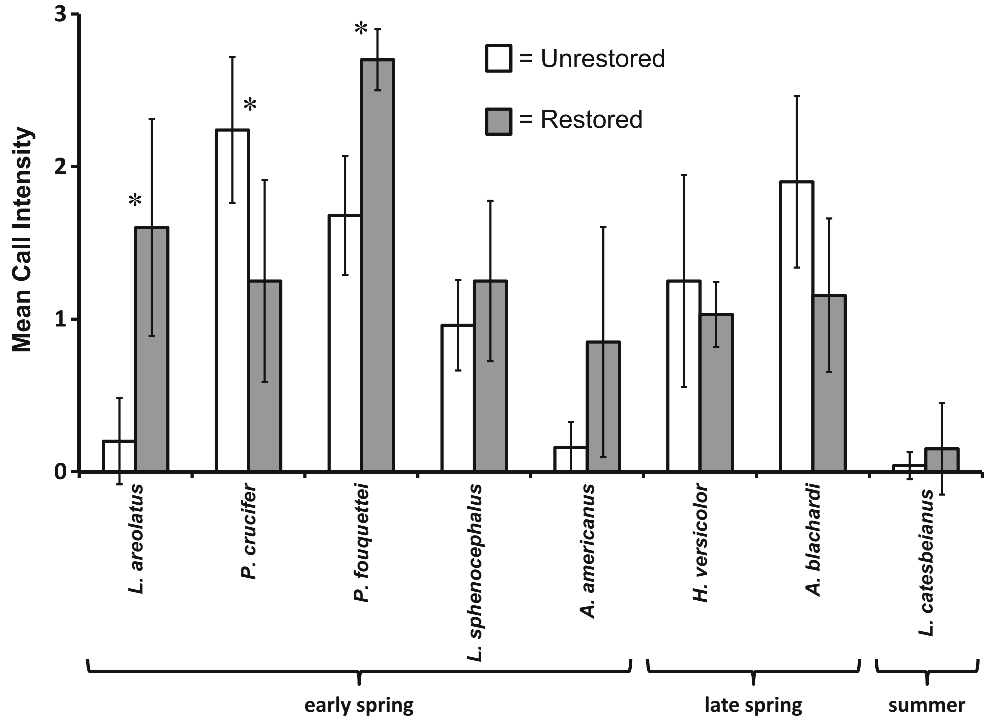

Fig. 2 Comparison of anuran call intensities in restored ($N = 4$) and unrestored ($N = 5$) prairie wetland units at Woolsey Wet Prairie Sanctuary, Arkansas, USA. Bars represent mean (±SD) call intensity; asterisks indicate statistical significance ($p \leq 0.05$) using wetland as the statistical unit

($t = 0.67$, d.f. = 5.66 $p = 0.528$; Fig. 3). Aquatic traps were also effective for sampling other wetland species, capturing a total of 134 *A. texanum* larvae, 8695 crayfish, and 14,154 Ranid tadpoles over 1090 trap-nights. Ranid tadpoles were found to have greater relative abundance in restored wetlands (Mann-Whitney *U* test, $U_{1,9} = 1$, $p = 0.009$; Fig. 4), whereas captures of *A. texanum* and crayfish were not significantly different among wetland types (crayfish: $U_{1,9} = 13$, $p = 0.78$; *A. texanum*: *t*-test, $t = 1.12$, d.f. = 5.03, $p = 0.312$).

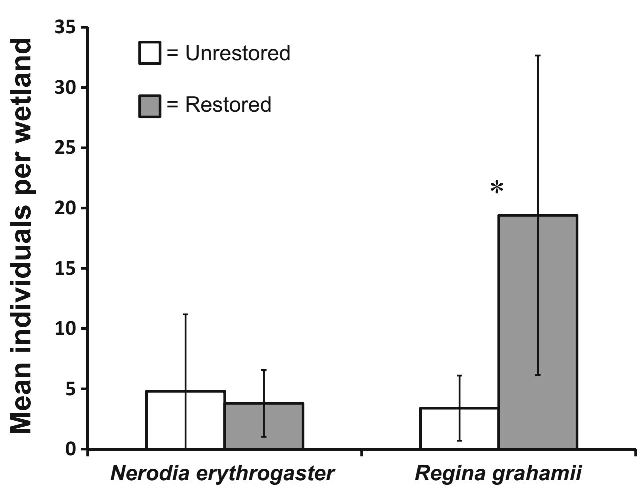

Fig. 3 Mean number of individual *N. erythrogaster* and *R. grahamii* captured in aquatic minnow-traps in restored ($N = 6$) and unrestored ($N = 5$) prairie wetlands at Woolsey Wet Prairie Sanctuary, Arkansas, USA. Bars represent mean (±SD) number of individual snakes captured per wetland during March – June, when equal effort was used in restored and degraded habitats. Asterisks indicate statistical significance ($p \leq 0.05$) using wetland as the statistical unit

Time-Constrained, Visual Encounter & Coverboard Surveys

We detected 22 species using a combination of coverboards and time-constrained visual surveys. Coverboard surveys were especially effective for detecting terrestrial snakes, such as *Pantherophis obsoletus* (Western Ratsnake), *Coluber constrictor* (North American Racer), *Lampropeltis calligaster* (Yellow-bellied Kingsnake), *Thamnophis sirtalis* (Eastern Gartersnake), and *T. proximus* (Fig. 5; Table 1), but were not effective at detecting the highly aquatic *R. grahamii*, compared to other techniques (e.g. minnow traps).

Among snake species with >20 detections under coverboards, *T. sirtalis* exhibited greater captures in degraded units, whereas *T. proximus* was captured in nearly equal numbers among habitats. Other species were infrequently encountered under coverboards, but most were captured slightly more frequently in unrestored habitats, the exception being *P. obsoletus*, which was only captured in unrestored units (Fig. 5; Table 1). While only captured incidentally during VES, *C. serpentina*, *T. scripta*, and *T. carolina* were encountered most frequently in restored units (Table 1).

Discussion

Our surveys of restored and unrestored remnant tallgrass prairie and associated wetlands at WWPS revealed high overall diversity and abundance of reptiles and amphibians, with documentation of most expected species that are not exclusive to heavily

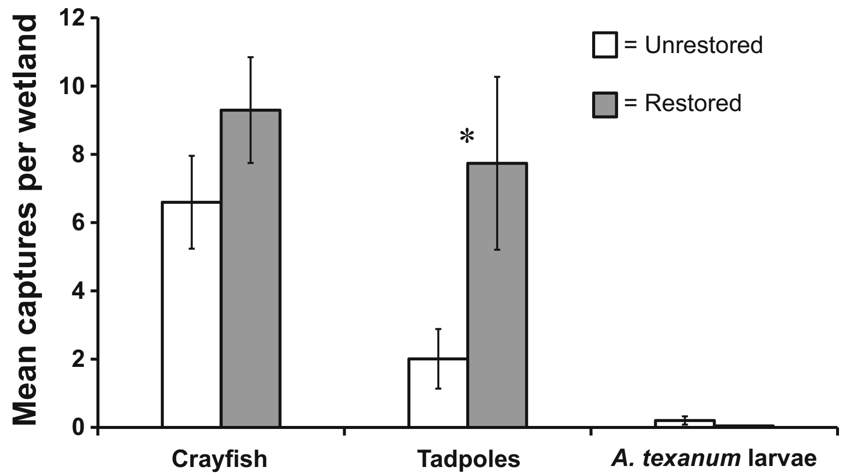

Fig. 4 Crayfish, tadpole, and larval *Ambystoma texanum* capture rates in aquatic traps set in restored ($N = 6$) and unrestored ($N = 5$) prairie wetlands at Woolsey Wet Prairie, Arkansas Sanctuary, USA. Bars represent mean (±SD) captures, standardized for trapping effort

forested, high-elevation, rocky, or stream habitats (Trauth et al. 2004). Species richness was similar among restored and unrestored habitats. Herpetofauna considered regionally uncommon and of conservation concern, such as *L. areolatus* and *R. grahamii*, showed preferential use of restored habitats. More common and widespread species like *N. erythrogaster*, *H. versicolor*, *L. catesbeianus*, and *L. sphenocephalus* were not found to use restored and unrestored habitats differentially. Proximity to extensive upland habitats and perhaps lagged population-level responses to restoration may explain higher relative abundances of terrestrial snakes and salamanders in unrestored units. Our findings demonstrate that species of conservation concern (*R. grahamii* and *L. areolatus*) may respond positively to tallgrass prairie and wetland ecosystem restoration and highlight important considerations when managing these habitats for conservation of herpetofauna. However, future studies should test the generality of our findings across larger special scales using rigorous analysis of species' patch occupancy dynamics, species richness, and population sizes in tallgrass prairie and associated wetlands. Such approaches require sufficient sample sizes and field and analytical methods that allow for quantification of species and individual detection probabilities (MacKenzie and Royle 2005; Schmidt and Pellet 2010).

Amphibians

Our study suggests that WWPS provides suitable habitat for *L. areolatus*. *Lithobates areolatus* were found in both restored and unrestored habitats, but were detected at a higher proportion of restored wetlands. Furthermore, *L. areolatus* calling intensity was greater in restored wetlands, suggesting that *L. areolatus* may breed preferentially in the restored wetlands. Although we were unable to differentiate between larval *L. sphenocephalus* and *L. areolatus*, greater relative abundances of *Lithobates* larvae in restored wetlands were also consistent with this conclusion. Preferential use of restored habitats was more apparent for *L. areolatus* than for *P. fouquettei*, *L. sphenocephalus*, and other syntopic anurans. These results suggest that restoration may be a viable conservation tool for *L. areolatus*, one of the most rapidly-declining North American

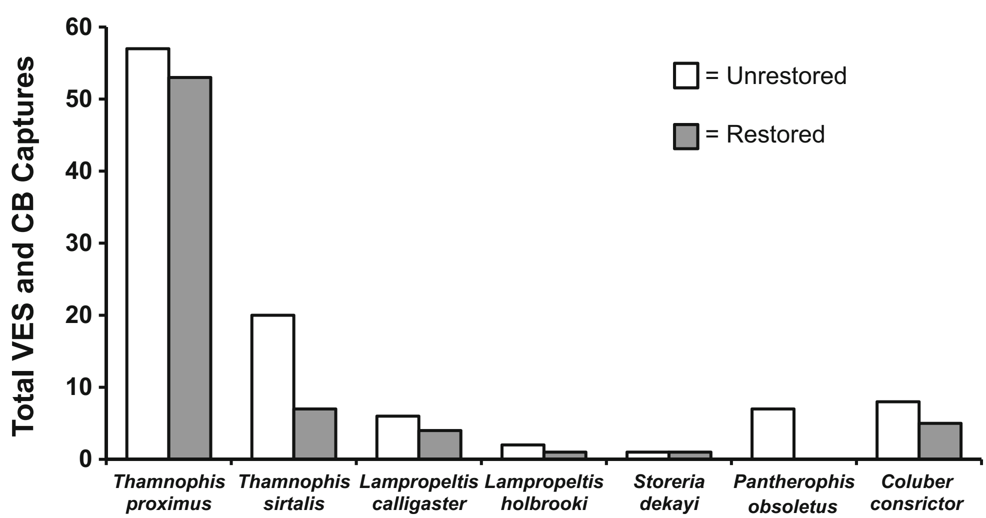

Fig. 5 Total snake captures during time-constrained visual encounter surveys and standardized coverboard surveys, February – November, 2014 in restored and unrestored habitat at Woolsey Wet Prairie Sanctuary, Arkansas, USA. Approximately equal effort was deployed in degraded and restored units

anurans (Lannoo et al. 2009; Engbrecht and Lannoo 2010; Engbrecht et al. 2012). Their pattern of decline is thought to be driven—at least initially—by wide-spread habitat loss and degradation, particularly the loss of wetlands due to drainage (Parris and Redmer 2005). Therefore, the presence of a breeding population of *L. areolatus* in Northwest Arkansas, where wetlands within tallgrass prairie habitat are rare, highlights the importance of habitat provided by WWPS.

Although suitable (fishless) aquatic breeding habitat is critical for *L. areolatus*, adults spend surprisingly little time in these habitats. Heemeyer et al. (2012) found that *L. areolatus* occupy upland habitats up to 1020 m from aquatic habitat for an average of 10.5 consecutive months per year. Therefore, upland habitat quality may be equally important for explaining observations of wetland usage by *L. areolatus*. *Lithobates areolatus* are philopatric crayfish burrow obligates, and upland habitat use during the non-breeding season reflects presence of crayfish burrows (which occur throughout the landscape) as core requirements for refuge from predators, foraging, aestivation, brumation, and access to groundwater (Hoffman et al. 2010; Engbrecht et al. 2012; Heemeyer et al. 2012). Reliance on both upland habitats with crayfish burrows and fishless wetlands for breeding has severely restricted the distribution of *L. areolatus* because increasing portions of their range are being subjected to agricultural and recreational practices (e.g. plowing, tilling, and wetland drainage; reservoir creation and wide-spread stocking of predatory fish; Parris and Redmer 2005) that degrade these habitats. Persistence of *L. areolatus* is likely predicated upon suitable hydroperiod provided by a matrix of depressional wetlands, availability of upland burrow habitats created by burrowing crayfish, and movement corridors between these habitats (Williams et al. 2012a; Engbrecht et al. 2013). Although it is clear that the restored wetlands at WWPS serve as important breeding habitat for *L. areolatus*, the extent to which adults migrate out of the sanctuary to access nearby upland habitats remains unknown. However, surveys during breeding events revealed >20 individuals crossing roads as they migrated into WWPS from adjacent private land, especially hayfields east of the sanctuary (Fig. 1). Thus, road mortality and development of adjacent land could negatively affect *L. areolatus* populations that breed within the sanctuary.

Interestingly, *A. texanum*, which are generally absent from the Ozark Plateaus and are typically associated with prairie habitats in Northwest Arkansas (Trauth et al. 2004; pers. obs.), were found in both habitat types with similar relative abundances. This pattern may simply reflect more generalist habitat preferences than were previously recognized for *A. texanum* in this region (Petranka 1998). Alternatively, *A. texanum* may require a longer time to respond to restoration activity than anurans.

Reptiles

Regina grahamii clearly exhibited a greater preference for restored habitat than syntopic aquatic and semiaquatic snakes. While mechanisms for this phenomenon are not known, we suggest features of the restored wetlands such as variable hydrology, vegetative structure, and abundance of crayfish burrows are implicated. *Regina grahamii* are dietary specialists, feeding almost exclusively on freshly molted crayfish (Mushinsky and Hebrard 1977) and exhibit a strong association with crayfish burrows, which they use as refuge from predators and as seasonal hibernacula (Gibbons and Dorcas 2004). Although crayfish relative abundance within the aquatic habitat was not significantly higher in restored sections, burrows in the unrestored units may be disturbed or destroyed during agricultural activities (mowing). *Regina grahamii* are known from only a few historic records in Northwest Arkansas (Conant and Collins 1998; Trauth et al. 2004), and this study has documented the first observations of this species in the region in nearly 60 years (Dowling 1957; Trauth et al. 2004). Despite the lack of records of *R. grahamii* in Northwest Arkansas, a relatively robust population apparently exists at WWPS (168 individuals captured in 2014). However, because *R. grahamii* are highly aquatic and extremely secretive, it is unclear if this population is truly disjunct, or belongs to a larger, previously undetected population extending westward into Oklahoma, USA. Although WWPS apparently provides excellent habitat, *R. grahamii* is considered a species of greatest conservation need in the state. Because this population of *R. grahamii* is likely isolated from surrounding populations, its persistence should be considered in future land management decisions.

Relative abundances of *N. erythrogaster* and *T. proximus*, which are semi-aquatic generalists, were similar in restored and degraded habitat. *Nerodia erythrogaster* was the most commonly encountered reptile in this study. It was captured in every wetland, as well as in a stream (Owl Creek) in the North Unit (Fig. 1; Table 1). Most terrestrial snake species occurred in somewhat greater relative abundances in the unrestored habitat. In the restored area, *T. sirtalis*, *L. calligaster*, *Lampropeltis holbrooki* (Speckled Kingsnake), and *C. constrictor* were captured infrequently in upland patches, while *P. obsoletus* was not detected at all. Thus, despite the suitability of the restored habitat at WWPS for aquatic snake species, species richness and abundance of terrestrial snake species and lizards may be higher in unrestored units that are in closer proximity to extensive dry uplands. This phenomenon highlights the importance of considering upland habitat in future restoration activities at the site. Alternatively, as posited for *A. texanum*, terrestrial reptiles could be experiencing a delayed response to the restoration. Bateman et al. (2008) monitored lizard communities in the Middle Rio Grande for 7 years following the experimental removal of non-native plants and found that some species only began to show substantial population responses in the final year, likely due to high year-to-year variation in precipitation. Continued monitoring of reptile communities at WWPS will address lags in response to ecosystem restoration and the degree to which species are limited by upland habitat availability.

Conclusions

This study has shown that active management of WWPS, including the use of prescribed fire, creation of ephemeral wetlands, and revival of relict vegetative communities, can benefit herpetofaunal communities and promote the persistence of two regionally uncommon species: *L. areolatus* and *R. grahamii*. We offer two recommendations to maximize the value of this site for conservation of rare and sensitive herpetofauna. First, restricting fish from colonizing wetlands is imperative. Presence of predatory fish, especially centrarchids (Herwig et al. 2013), in the wetlands could decimate larval amphibian and crayfish populations (Hecnar and M'Closkey 1997), and wetlands with permanent to semi-permanent hydrology are at greatest risk of developing fish populations via surface water flow or animal-mediated egg deposition (Snodgrass et al. 1996). Additionally, increasing the extent of protected, high quality upland habitat would be highly beneficial for herpetofauna at WWPS, and should be a high priority in future management activities.

Based on our research, WWPS appears to currently provide habitat that supports a rich community of herpetofauna. However, it is uncertain if this diversity is secure, given the small (16.6 ha.) size of the protected area, the sprawling development in this rapidly-growing region (Knutson et al. 1999), and the erosion of diversity expected with decreasing patch size (MacArthur and Wilson 1967). Our results also demonstrate that former prairie habitats degraded by human activity may support species of conservation concern, along with more common and widespread species (Mushet et al. 2012, but see Knutson et al. 2004). Thus, lightly degraded prairie habitats (e.g., hayfields and lightly grazed cattle pastures) may be important for maintaining relict populations, promoting connectivity among fragmented higher-quality habitat patches, and should be targets for future restoration (Lannoo et al. 2017; Stiles et al. 2017). It is currently unknown if prairies that have undergone other forms of habitat alteration, such as urban or residential development, are capable of supporting relict populations. Therefore, continued research and development of management plans for *L. areolatus* and *R. grahamii* at WWPS is warranted.

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