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Environmental Management

ISSN 0364-152X

Environmental Management
DOI 10.1007/s00267-014-0355-2



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Grassland Fire and Cattle Grazing Regulate Reptile and Amphibian Assembly Among Patches

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Received: 22 December 2013 / Accepted: 14 August 2014
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Abstract Fire and grazing are common management schemes of grasslands globally and are potential drivers of reptilian and amphibian (herpetofauna) metacommunity dynamics. Few studies have assessed the impacts of fire and cattle grazing on herpetofauna assemblages in grasslands. A patch-burn grazing study at Osage Prairie, MO, USA in 2011–2012 created landscape patches with treatments of grazing, fire, and such legacies. Response variables were measured before and after the application of treatments, and I used robust-design occupancy modeling to estimate patch occupancy and detection rate within patches, and recolonization and extinction (i.e., dispersal) across patches. I conducted redundancy analysis and a permuted multivariate analysis of variance to determine if patch type and the associated environmental factors explained herpetofauna assemblage. Estimates for reptiles indicate that occupancy was seasonally constant in Control patches ($\psi \sim 0.5$), but declined to $\psi \sim 0.15$ in patches following the applications of fire and grazing. Local extinctions for reptiles were higher in patches with fire or light grazing ($\varepsilon \sim 0.7$) compared to the controls. For the riparian herpetofaunal community, patch type and grass height were important predictors of abundance; further, the turtles, lizards, snakes, and adult amphibians used different

patch types. The aquatic amphibian community was predicted by watershed and in-stream characteristics, irrespective of fire or grazing. The varying responses from taxonomic groups demonstrate habitat partitioning across multiple patch types undergoing fire, cattle grazing, and legacy effects. Prairies will need an array of patch types to accommodate multiple herpetofauna species.

Keywords Herpetofauna · Heterogeneity · Metacommunity ecology · Patch-burn grazing · Prairie · Occupancy model

Introduction

Understanding species distribution is a central ecological principle and can predict wildlife responses to human disturbances. Habitat heterogeneity may be an important factor for species distribution, and human disturbance can increase or decrease landscape heterogeneity (e.g., August 1983; Tews et al. 2004; Morrison et al. 2006). The metacommunity concept is a novel theory for community ecology (Leibold et al. 2004; Holyoak et al. 2005) that searches for the underlying factors and mechanisms responsible for animal distribution and dispersal in response to local environmental conditions. To date, both experimental and observational metacommunity studies have underrepresented macro-organisms and terrestrial ecosystems, particularly amphibians, reptiles, and grasslands (Logue et al. 2011).

Herpetofauna (amphibians and reptiles) make excellent models to examine ecological and metacommunity perspectives. First, they are aquatic-terrestrial linkages and small patch sizes (<10 ha) can provide substantial herpetofaunal biomass to support other trophic levels in the

Electronic supplementary material The online version of this article (doi:10.1007/s00267-014-0355-2) contains supplementary material, which is available to authorized users.

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aquatic and adjacent habitats (Deutschman and Peterka 1988; Regester et al. 2006). Secondly, herpetofauna are highly susceptible to environmental change relative to other taxa (Rowe et al. 2003) and responses to environmental management can be measured as changes in community structure in short-term experiments (Duellman 1989). Despite the importance of herpetofauna in ecological settings and research, amphibians and reptiles are under threat of extinction from habitat alterations and are often data deficient (Stuart et al. 2004; Böhm et al. 2013).

Tallgrass prairie and other grasslands have exceptional habitat modifications and undergo intensive land management. Grasslands historically dominated 25 % of the global terrestrial area (Dodds 1997), but today most are converted to row-crop agriculture or are fragmented parcels (Briggs et al. 2005). The predominant tallgrass prairie management tools are fire and grazing, which are essential for grassland maintenance and enhancing diversity (Stewart 1951; Harrison et al. 2003). Today, the prevailing tallgrass prairie management regime is annual fire and high-stock cattle grazing (densities of 0.8 animal units/ha or greater; Derner et al. 2006) across large landscapes. Patch-burn grazing (PBG) is a new management technique designed to mimic the historical grassland regime with fire–grazer interactions by creating heterogeneous patches in space and time (Fuhlendorf and Engle 2004). The PBG approach is being progressively adopted and promoted on public and private lands due to its conservation benefits of promoting terrestrial plant and wildlife diversity (e.g., Fuhlendorf et al. 2006, 2010; Engle et al. 2008). Given that native grasslands are endangered ecosystems experiencing new management such as PBG, research is needed to understand its effects to herpetofauna distribution and diversity.

Despite fire and grazing are characteristic of grasslands, few studies have addressed its consequences to herpetofauna. This lack of research is surprising due to the moderately high diversity of herpetofauna in prairies. For example, tallgrass prairie is habitat for at least 17 amphibian and 25 reptile species (Johnson 2000), and most of these species have large ranges that expand across eastern and central North America that encompass several biomes (Conant and Collins 1998). Studies thus far focused on a single species (e.g., collared lizards; Blevins and With 2011), a single management technique, usually fire (e.g., Cavitt 2000; Wilgers and Horne 2006), and/or other biomes (e.g., Argentinean grasslands; Cano and Leynaud 2009, montane forests of North America; Pilliod et al. 2003, and Australian arid-woodlands; James 2003).

The potential negative impacts of fire and grazing on herpetofauna are many. The spring breeding season, peak activity, and dispersal of herpetofauna overlap the fire and grazing season in tallgrass prairie. Direct mortality of herpetofauna from fire is well documented (e.g., Russell

et al. 1999). Vegetation structures (such as grass height and litter depth) in grasslands are reduced by both burning and grazing; a decrease in vegetation can decrease soil moisture and negatively affect the skin respiration capacity of amphibians (Duellman and Trueb 1994). Further, reduced vegetative cover could make herpetofauna vulnerable to predation and high temperatures (Seebacher and Alford 2002). Further, cattle can increase nitrogenous waste and sediment yields to aquatic systems, both of which can negatively impact amphibian larval development, survival, and post-metamorphic recruitment (Rouse et al. 1999; Schmutzer et al. 2008). Despite the potential negative consequences, fire and grazing are natural processes that grassland herpetofauna have presumably co-evolved with, and mechanisms such as resource partitioning (Toft 1985) or rescue effects (Brown and Kodric-Brown 1977) could allow herpetofauna to withstand or overcome these processes.

The goals of this study were to determine how the herpetofauna assemblage responded to fire, cattle grazing, and legacy effects in tallgrass prairie undergoing PBG. I estimated and compared herpetofaunal occupancy (ψ), detection (P), local recolonization (γ), local extinction (ϵ), abundance, and species richness (S) among patches from repeated field surveys, both before and after PBG. I also related herpetofaunal assemblages to patch types and the associated habitat characteristics, such as vegetation structure and water quality. The landscape mosaic from PBG allowed testing whether the data fit the *species-sorting perspective* within the metacommunity concept, which states that patch quality and animal dispersal will affect community composition (Leibold et al. 2004).

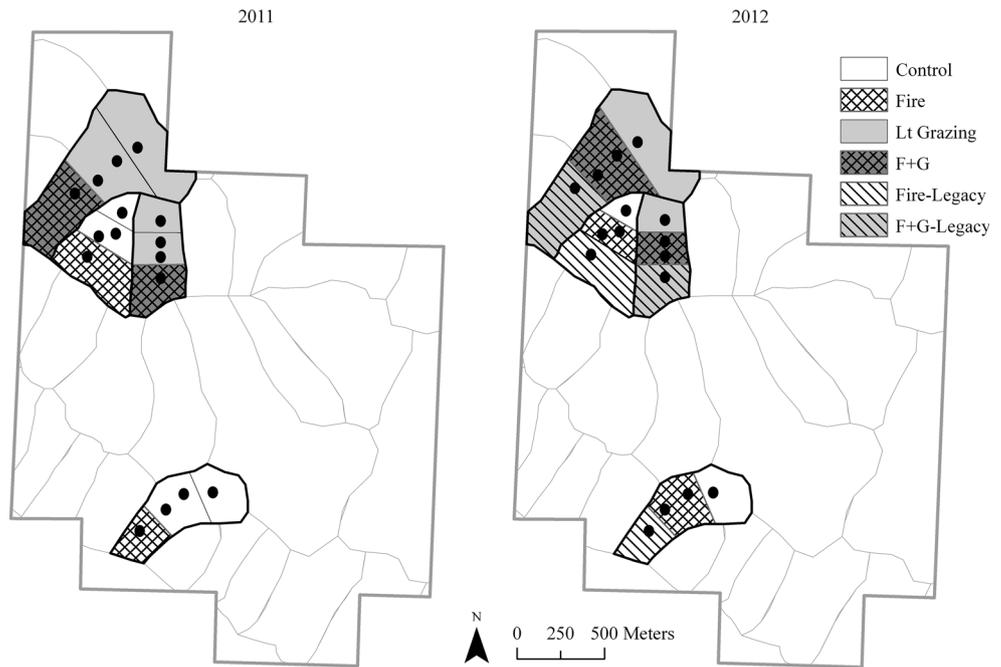
I hypothesized that herpetofauna occupancy, abundance, and richness would be lowest in patches with fire and cattle grazing because these habitats would be unsuitable or unfavorable. Similarly, I expected patch extinction to increase in patches following fire and/or grazing, either because herpetofauna would behaviorally avoid those patches and/or experience greater mortality. Lastly, I suspected herpetofauna would respond differently depending on taxonomy (i.e., order, class, or species), and therefore examined responses at a variety of taxonomic levels.

Methods

Study Site and Design

This study encompassed four small watersheds (10–54 ha) at Osage Prairie Conservation Area near Nevada, MO, USA (Fig. 1). Each stream in the watershed was a first-order, intermittent stream typically flowing from fall to early summer. Prior to the PBG experiment, the watershed

Fig. 1 Landscape patches at Osage Prairie, MO, USA. Four watersheds were divided into three patches each (studied watersheds outlined in *bold*). Every patch was labeled one of six patch types: Control (no fire or grazing in last 5 years), Fire, Lt Grazing (light cattle grazing), Fire-Legacy (burned the previous year), F+G-Legacy (burned and grazed previous year), and F+G (burned and grazed during sampling). Permanent sampling plots are indicated by the *black dots* and are within the stream's 10-m-riparian zone. Patch type changed in every patch from 2011 to 2012



and stream characteristics were similar within and across study sites (Larson et al. 2013a), and therefore I expected differences in animal assemblages to reflect applied treatments. All watersheds were completely encompassed by native tallgrass prairie and past management included prescribed burning approximately every 5 years, triennial haying in small patches, and the occasional removal of riparian trees >10 cm in diameter (Missouri Department of Conservation, personal communication).

Beginning April 2011, Osage Prairie watersheds underwent a designed PBG experiment. Each studied watershed was burned mid-April with one-third of the watershed burned (Fig. 1). Two watersheds had yearling calves stocked at a density of ~ 0.42 animal units/ha (where one animal unit = 227–363 kg). Cattle were on pasture from 1 May to 31 July each year. In 2012, treatments were applied to different patches nested within watersheds. Six patch types were created: (1) Control (with no fire or grazing in the last 5 years); (2) Fire (patch burned in spring); (3) Lt Grazing (light cattle grazing beginning \sim May 1); (4) F+G (fire in spring, followed by heavy cattle grazing \sim May 1); (5) Fire-Legacy (patch burned the previous year; no fire or grazers in the sampled year); and (6) F+G-Legacy (F+G the previous year; none in the sampled year). Within each patch, there were one or two permanent plots for repeated sampling of herpetofauna (Fig. 1). The maximum Euclidean distance between adjacent plots was 2 km and averaged 600 m apart, which is greater than most herpetofauna dispersal capabilities (Smith and Green 2005).

Animal Surveys

I surveyed for herpetofauna in March–May 2011 and 2012. All surveys were within a 10-m-riparian zone and standardized at each plot. Sampling occurred at each plot, two to three times per month but within 2 days of each other to meet population closure assumptions for occupancy modeling. To ensure dispersal was not simply an artifact of the breeding season or seasonal succession of vegetation, I monitored Control patches throughout time to compare to estimates from treated patches. In each sampling date, the plots were randomly ordered for sampling to reduce the “time of day” effect. To eliminate observer bias in herpetofaunal detection, I was the sole person conducting the surveys.

I used four methods to capture an array of herpetofauna species. First, two minnow traps were deployed in streams in each plot for 16–20 h to capture tadpoles, salamander larvae, and any swimming adults. Second, coverboard arrays of 16 plywood boards were arranged in 2 rows as artificial refugia (Heyer et al. 1994). At least 3 months prior to sampling, the boards were weathered in situ (Dodd Jr. 2010). Finally, visual encounter surveys (VES) were conducted along three permanent transect lines of 40 m each (Heyer et al. 1994). The VES transects were placed 0 m (water’s edge), 2 m, and 9 m parallel to the streamside. A day before prescribed fires, I removed all survey equipment from the burn zone and replaced them hours following the burn in the original location. The equipments were left to rest for 2 days before sampling to allow recolonization.

Once captured, I collected information regarding species, age class, and a photograph. All captured animals were released at the exact point of capture after the survey was completed (max. 0.5 h holding time). All institutional, legal, and national guidelines for the care and ethical use of animals were followed.

Habitat Variables

I sampled two distinct habitat types: aquatic habitats (one stream per watershed) and riparian habitats (one per plot). These habitats correspond to either the aquatic community (i.e., adult amphibians and tadpoles), or to the riparian community (i.e., adult amphibians and reptiles on land). The habitat data were used as predictor variables for the aquatic and riparian community structures.

I collected riparian vegetation data during each sampling period within each plot, which included ground cover (bare or grass), percent cover, litter depth, and grass height. Vegetation structure data were collected along two 10-m transects perpendicular to the stream, with a 1×5 m plot every 5 m along the transect (Daubenmire 1959). Data were averaged for each transect and associated with riparian fauna found in that plot. Further, I conducted an analysis of variance (ANOVA), followed by Tukey's Honestly Significant Difference post hoc test, to determine if vegetation structures differed among the six patch types.

I collected the following habitat information for the aquatic community (amphibians captured in-stream): (1) average water depth, (2) substrate type (silt or rock), (3) percent riparian canopy cover, and (4) percent in-stream vegetation. Habitat information was collected and averaged for a 1×3 m plot in the stream where the amphibian was captured.

Additionally, I collected and processed stream water (APHA 1995) to obtain total suspended solids (TSS) and ammonium (NH_4^+) concentrations to relate to amphibian tadpole abundance. Previous studies suggested that high concentrations of TSS and NH_4^+ can hinder tadpole development (Rouse et al. 1999; Schmutzer et al. 2008) and that cattle can increase these water quality variables (Belsky et al. 1999). From 2009 to 2012, I collected monthly water samples at the base of each watershed in acid-washed bottles from the thalweg and stored on ice. The NH_4^+ samples were filtered within 24 h (Whatman GFF, 0.7 μm retention) and then frozen at -30 °C until analyzed using an OI-Analytical Flow Solution IV auto-analyzer (Xylem Inc., White Plains, USA). For TSS, 1 L of water was filtered through pre-combusted, pre-weighed glass-fiber filters (GFC Whatman, 1.2 μm retention) within 24 h, and the filters with retained material were dried at 60 °C and weighed to calculate TSS. I used a Student's t test to determine if the TSS and NH_4^+ concentrations differed between PBG and ungrazed streams.

Species Richness

I calculated species richness for reptiles and amphibians across patch types, watersheds, and sample years. Richness was the total number of species detected during the treatment period ($n = 6$ sample dates). Using ANOVA and Tukey's HSD post hoc test, I compared richness of the six patch types, across watersheds, and sample years.

Redundancy Analysis

The objective of the redundancy analysis (RDA) was to relate herpetofauna abundance, land management treatments, and measured environmental variables. A RDA is an extension of multiple regression where the ecological community (Y) is constrained by linear combinations of the predictor variables (X ; Legendre and Legendre 1998). The response variables (i.e., the aquatic or riparian community) are taxonomic order or species abundances, and the predictor variables include patch type and the measured environmental characteristics.

I conducted two separate RDAs for the riparian community and the aquatic community. All response variables (i.e., species abundance data) were Chord transformed because this produced the highest amount of variation explained (Legendre and Gallagher 2001). The measured environmental predictor variables (i.e., the RDA terms) for the riparian community included: *year* (categorical; 2011 or 2012), *patch type* (categorical; Fire, F+G, Lt Grazing, Control, Fire-Legacy, or F+G-Legacy), *grass height* (continuous), *% grass cover* (continuous), *ground cover type* (categorical; bare or grass), and *litter depth* (continuous). The aquatic community's measured environmental predictors included: *year* (categorical; 2011 and 2012), *patch type* (categorical; Fire, F+G, Lt Grazing, Control, Fire-Legacy, or F+G-Legacy), *watershed* (categorical; stream 1, 2, 3, or 4), *water depth* (continuous), *% in-stream vegetation cover* (continuous), *% riparian canopy cover* (continuous), *TSS* (total suspended solids; continuous), and *NH_4^+* (ammonium; continuous). The variance inflation factors found no redundancy in either model ($\text{VIF} < 10$), so all predictor variables were included. Using R 2.14.1 (2011, R Development Core Team, Vienna, Austria) and the *vegan* package (Oksanen et al. 2011), I conducted a permuted ($\text{perm} = 9,999$) multivariate analysis of variance (PERMANOVA) to assess the significance of the overall RDA models, RDA axes, and RDA terms.

Robust-Design Occupancy Modeling

The goal of this analysis was to estimate occupancy (ψ) and detection (P) within a patch, and the rates of extinction (ϵ) and recolonization (γ) across patches (MacKenzie et al.

2002). Occupancy is a state variable that can be used as a response variable to assess the suitability of habitats; in this case, I compare herpetofaunal use for multiple patch types. Occupancy modeling is necessary if detection is imperfect, and the detection estimate will be a correction factor to give a less biased estimation of the true occupancy level (Royle et al. 2005). The dispersal estimates (ϵ and γ) and changes in patch occupancy are response variables that infer animal response to treatments. The robust-design occupancy model (or multi-season occupancy model) provides the four parameter estimates (ψ , P , ϵ , γ) based on detection/non-detection data. Parameter estimates for ψ and P are obtained for each of the primary seasons, and ϵ and γ are transition probabilities between primary seasons (see conceptual diagram in Online Resource 1). The four parameters are defined as follows: Occupancy (ψ) is the probability that a randomly sampled plot is occupied by a species (i.e., a species is detected and accurately identified in a sampled plot). Detection (P) is the probability that an animal is captured, given it is present, at a plot. Extinction (ϵ) is the probability that an occupied plot in season t is unoccupied in season $t + 1$. Recolonization (γ) is the probability that an unoccupied plot in season t is occupied in season $t + 1$.

The encounter history matrix pooled all reptile species, capture methods, and patches of the same type, but was separated by sample years 2011 and 2012 to increase the degrees of freedom and obtain quality parameter estimates. This pooling tactic was required to run the model because of low sample sizes for most species (Online Resource 2). Further, I attempted to use the robust-design occupancy model for two species with the greatest abundance (*Scincella lateralis* and *Terrapene ornata*) and for each the three taxonomic groups (turtles, lizards, and snakes) but the models contained many inestimable parameters, signifying that data must be pooled into one guild (reptiles) for occupancy analysis. Occasionally, program MARK yielded nonsense parameters due to low numbers of animals for this “data hungry” modeling approach. Nonsensical parameter estimates and those in which the standard error was greater than the estimate are excluded from the “Results” section and indicated by “NA” in Fig. 4. No formal goodness-of-fit test exists (MacKenzie et al. 2003), so I assumed over-dispersion was negligible.

The sampling design included treatments applied through time, and a treatment corresponds to a new primary season in the model. For simplicity, I only include four patch types for occupancy analysis: (1) Control, (2) Fire, (3) Lt Grazing, and (4) F+G. In this study, a primary season (S) is delineated by the application of treatments and corresponds to the months of March–May. So, S_1 is prior to any fire or grazing (Control season; March), S_2 is following the application of fire (Fire season; April), and

S_3 is following the application of fire and grazers (F+G season; May). Across primary seasons (i.e., as treatments are applied), the model assumes an open population allowing for recolonization and extinction across patches. I predicted herpetofauna may respond to treatments via dispersal across patches, so therefore I estimated γ and ϵ between each primary season.

I used the robust-design occupancy model using program MARK v.6.2 and an information–theoretic approach (i.e., Akaike’s Information Criterion adjusted for small sample size (AIC_c); Burnham and Anderson 2002). This model evaluated which of the a priori model(s) best explained the relationship between the predictor variables (i.e., time, treatment, and interaction) and the response variables of occupancy and dispersal. Although covariates can be included in the AIC_c models, the potential combinations for a priori models with covariates were immense, so driving environmental factors were identified by multivariate procedures instead. To date, occupancy models rarely include spatial parameters (MacKenzie 2006), and are typically designed for specific data structures or have low model performance under certain conditions (e.g., low occupancy probabilities). Due to these constraints, spatial parameters were not modeled for this dataset. The top models were selected and considered parsimonious according to three criteria (Burnham and Anderson 2002; Johnson and Omland 2004; Arnold 2010): the AIC_c < 2 and did not contain uninformative parameters, the model(s) had high Akaike weights and evidence ratios. Parameter estimates were taken from the top AIC_c model. The a priori candidate models are in Online Resource 3.

Results

Captures

Across 2 years, I captured a total of 150 reptiles representing 14 species. The common reptiles were the Ground Skink (*Scincella lateralis*), Ornate Box Turtle (*Terrapene ornata*), and Garter Snake (*Thamnophis sirtalis*). In total, I captured 1,045 amphibians of 10 species. Southern Leopard Frog (*Rana (Lithobates) sphenoccephala*) and American Toad (*Bufo americanus*) tadpoles dominated these counts (Online Resource 2).

Habitat Changes from Treatments

All the measured vegetation structures differed among patch types: % cover ($F_{(5,26)} = 16.72$, $P < 0.001$), litter depth ($F_{(5,26)} = 87.19$, $P < 0.001$), and grass height ($F_{(5,26)} = 7.68$, $P = 0.010$). In general, the Control and Lt

Grazing patches had the greatest *grass height*, *litter depth*, and *% cover*, and the patches with Fire and F+G had significantly less vegetation. The Fire-Legacy and F+G-Legacy patches had greater *grass heights* and *% cover* than the Fire and F+G patches, which shows a vegetation recovery trajectory from the previous years' fire and grazing (Online Resource 4). These results justify the demarcation of the six patch types.

TSS were similar at all watersheds prior to treatments ($t_{(1,28)} = 2.92$, $P = 0.879$) with a mean of 5 mg/L-TSS. The prescribed fire did not influence TSS at any stream ($t_{(1,11)} = 1.39$, $P = 0.196$). However, following the introduction of cattle to the two grazed watersheds, the mean TSS increased fourfold (mean 20 mg/L, max 75 mg/L).

Ammonium (NH_4^+) concentrations did not vary by watershed for 2 years before PBG ($t_{(1,28)} = 1.06$, $P = 0.385$) or following prescribed fire ($t_{(1,11)} = 0.59$, $P = 0.829$). Following PBG, mean NH_4^+ tripled at PBG watersheds (mean 80 $\mu\text{g/L}$, max 624 $\mu\text{g/L}$; $t_{(1,28)} = 2.60$, $P = 0.010$; Online Resource 5).

Fire Mortality

I surveyed four burned patches within 1 day of the fire on 20 March 2011 and observed six dead and burnt turtles. Two carcasses were identified as Ornate Box Turtles (*T. ornata*), one as a Western Painted Turtle (*Chrysemys picta bellii*), and three were not identifiable to species because of the burn severity. I was not able to fully assess fire mortality for snakes, lizards, and amphibians due to small body sizes, large burn patches, and the possibility of scavengers.

Species Richness

Across all patches and years, I captured 14 reptile species (Online Resource 2). Reptile species richness per *patch type* had a mean of three species and a maximum of eight species (Online Resource 6). Richness for reptiles was influenced by *patch type* ($F_{(5,14)} = 3.31$, $P = 0.035$), with the Control and Lt Grazing patches containing slightly fewer species than patches with fire or grazing in the last 2 years. Reptile richness was not influenced by *watershed* ($F_{(3,18)} = 0.46$, $P = 0.518$) or *year* sampled ($F_{(1,18)} = 3.15$, $P = 0.092$).

In total, I captured ten amphibian species (Online Resource 2). Amphibian richness was not affected by *patch type* ($F_{(5,14)} = 0.435$, $P = 0.817$), *watershed* ($F_{(3,18)} = 0.44$, $P = 0.180$), or *year* ($F_{(1,18)} = 3.65$, $P = 0.072$). In a patch, the mean richness of amphibians was two species with a maximum richness of five species (Online Resource 6).

Riparian RDA

A permutation test for the riparian RDA revealed the full model was highly significant ($F_{(12,26)} = 6.46$, $P = 0.005$). The first two axes of the full RDA model were significant (RDA1 ($F_{(1,35)} = 66.98$, $P = 0.004$) and RDA2 ($F_{(1,35)} = 36.57$, $P = 0.005$)), and cumulatively these axes explained 74 % of the variance in community structure. The PERMANOVA identified *patch type* ($F_{(5,22)} = 4.59$, $P < 0.001$) and *grass height* ($F_{(1,26)} = 3.11$, $P = 0.048$) as significant predictors of the riparian community (Online Resource 7).

Graphically, the RDA showed substantial structure for patch types, environmental variables, and riparian community associations (Fig. 2). The patch type Fire-Legacy clustered well in ordination space, with a strong association with snakes and high *% cover* (70–100 % grass). Turtles were tightly associated with tall *grass heights* (30–75 cm) and linked with the Lt Grazing treatment. Lizard abundance varied by *year*, with year 2012 having greater catches. Lizards were closely connected with the Fire, F+G, and F+G-Legacy treatments, which had *bare ground cover* and shallow *litter depth* (0–17 mm). Adult amphibians were positively loaded on RDA1 concomitant with tall *grass heights* and high percentages of *grass cover*. Complete *grass cover* (100 %) and deep *litter depths* (21–55 mm) were characteristic of the Control patches, but no taxonomic group selected for this treatment.

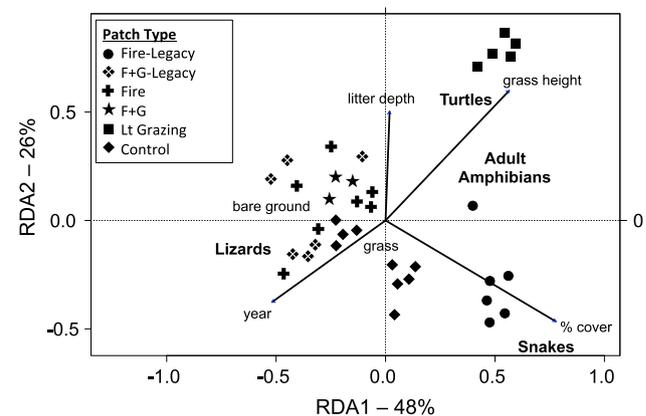


Fig. 2 A RDA triplot for the riparian community (turtles, snakes, lizards, and adult amphibians) from Osage Prairie, MO in 2011 and 2012. The animals were captured across six patch types indicated by *symbols*; the environmental factors are in *lower caps*; and the taxonomic groups are *bolded*. The full RDA model was highly significant ($P = 0.005$), as were axes RDA1 ($P = 0.004$) and RDA2 ($P = 0.005$). A PERMANOVA identified significant terms: treatment/patch type ($P < 0.001$) and grass height ($P = 0.048$)

Aquatic RDA

The full aquatic RDA model was significant ($F_{(18,55)} = 1.46$, $P = 0.051$), as were the first two axes (RDA1, $F_{(1,23)} = 19.86$, $P = 0.005$; RDA2, $F_{(1,23)} = 7.44$, $P = 0.005$) which explained 44 % of the variation in aquatic community structure. The RDA triplot showed little structure regarding treatments, environmental factors, and the aquatic community (Fig. 3). Adult amphibians showed a

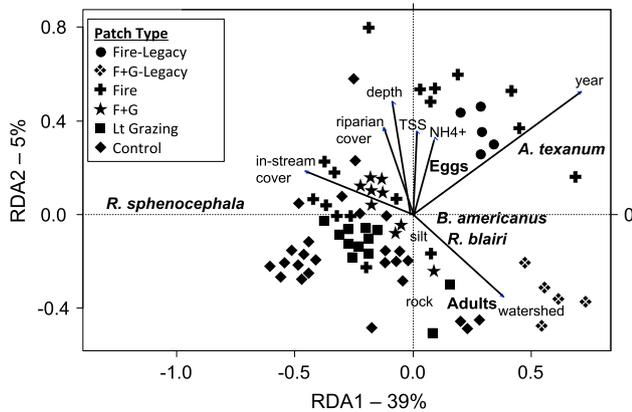


Fig. 3 A RDA triplot for the aquatic community from Osage Prairie, MO in 2011 and 2012. The taxonomic groups are *bolded* and included *Rana (Lithobates) sphenocephalus* tadpoles, *Rana (Lithobates) blairi* tadpoles, *Ambystoma texanum* salamander larvae, *B. americanus* tadpoles, egg masses, and adult amphibians (includes multiple species). The aquatic amphibians were captured across six patch types indicated by *symbols* and the environmental factors are in *lower caps*. The full RDA model was significant ($P = 0.005$), as were the axes (RDA1, $P = 0.005$; RDA2, $P = 0.005$). A PERMANOVA identified significant terms: year ($P < 0.001$), watershed ($P = 0.002$), in-stream cover ($P = 0.007$), and substrate type ($P = 0.029$)

high affinity for *watershed*. All watersheds had adults detected; however, one watershed (with PBG) was occupied by 60 % of the adults, likely because the watershed also contained two breeding ponds. The PERMANOVA found the variables *year*, *watershed*, *in-stream cover*, and *substrate* to be significant predictors (Online Resource 7).

Robust-Design Occupancy Modeling

AIC_c identified a single, most parsimonious model regarding reptile occupancy, detection, and dispersal with a high Akaike weight ($w_i = 0.89$; Online Resource 3). The top AIC_c model determined that occupancy and extinction were interactive effects of patch type and time, whereas detection and recolonization increased through time. The 95 % confidence intervals for occupancy and detection were narrow but were large for dispersal estimates.

Occupancy (ψ) of reptiles corresponded to a patch type and time interaction. The ψ in the Control patches hovered between approximately 40 and 50 % across all primary seasons but without trend (Fig. 4a). Conversely, ψ in the Fire and Lt Grazing patches decreased rapidly by ~50 % when treatments were applied (Fig. 4b, c). In the F+G patches, ψ was at the lowest estimate of only 13 % during Season 3 after fire and grazers were applied (Fig. 4d).

Extinction probability (ϵ) was an interaction of patch type and time. Unfortunately, the Control and F+G patches contained inestimable parameters. For the Lt Grazing patches, the extinction probability transition 2 occurs before the introduction of grazers but still shows a likely effect from the prescribed fires (Fig. 5a). The Fire patches had a ~20 % increase in ϵ during seasonal transition 2 following the prescribed fire (Fig. 5c).

Fig. 4 The estimate and 95 % confidence intervals for reptile occupancy (ψ) in spring 2011 and 2012 at Osage Prairie, MO across seasons, where Primary Season 1 corresponds to ~March, Primary Season 2 to ~April, and Primary Season 3 to ~May. The highest ranked AIC_c model included patch type and time effects ($g \times t$). NA indicates inestimable parameters

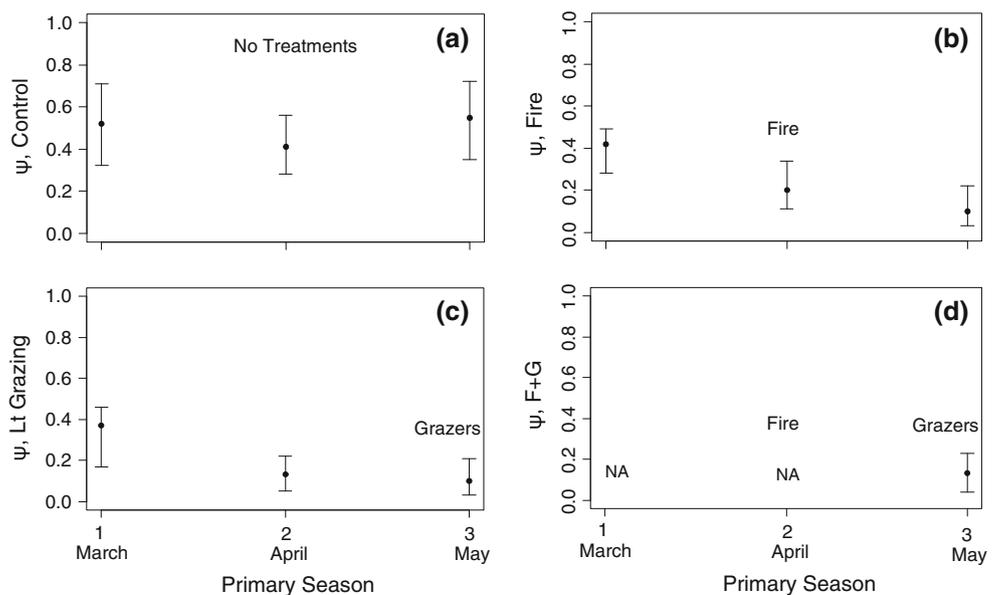
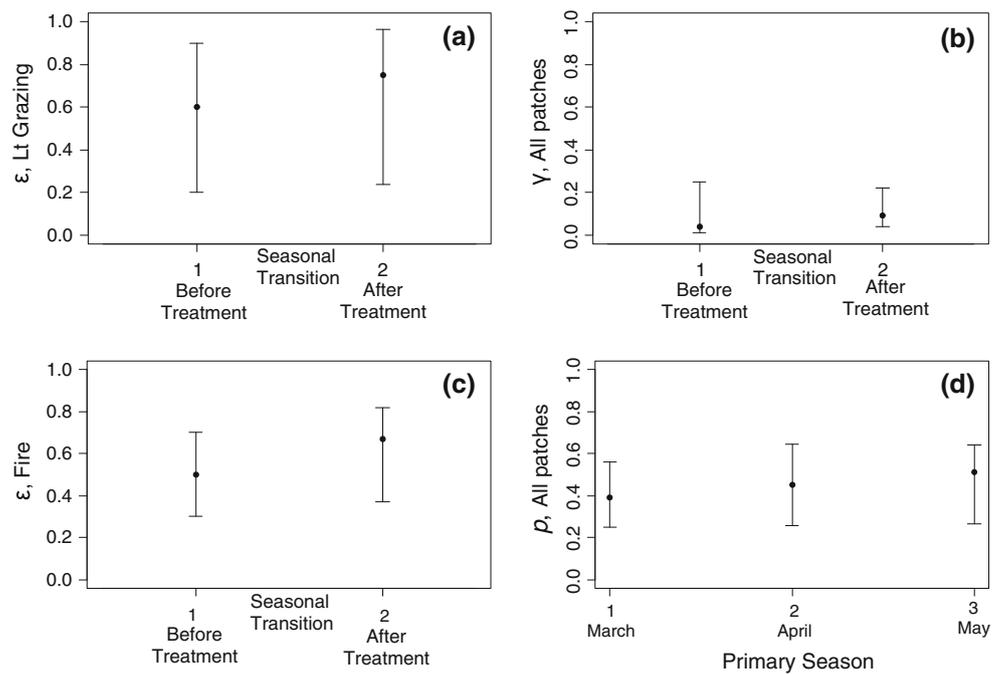


Fig. 5 The estimate and 95 % confidence intervals for reptile extinction (ε), recolonization (γ), and detection probability (P) in spring 2011 and 2012 at Osage Prairie, MO across seasons, where Primary Season 1 corresponds to ~March, Primary Season 2 to ~April, and Primary Season 3 to ~May. The highest ranked AIC_c model for ε included patch type and time effects (but two patch types were inestimable); and the highest ranked AIC_c model for γ and P included time effects only



Recolonization (γ) was a function of time (and not patch) but increased only ~10 % (Fig. 5b). Detection (P) estimates ranged from 40 to 50 %, and increased marginally through time in all patch types (Fig. 5d). The slight increase in P and γ suggests either my reptile capture ability improved with time, or these parameters are functions of reptile abundance as animals are more likely active and detected in Season 3.

Because amphibian abundance did not differ among patch types as indicated by the RDA and PERMANOVA (Fig. 3), I did not expect to find occupancy or dispersal differences and did not proceed with occupancy modeling for the aquatic amphibian community.

Discussion

This is the first experiment that revealed responses of grassland herpetofauna to PBG across space and time. Although this study occurred in tallgrass prairie, a rare and endangered ecosystem today, these 28 herpetofauna species have large geographical ranges across North America (Johnson 2000) and regularly experience prescribed fire and livestock enterprise, making results of this study widely applicable. To my knowledge, this is only experimental study to use robust-design occupancy modeling where the “primary seasons” are before and after land management treatments. This analytical approach has potential for similar wildlife applications or to quantify dispersal in response to other management techniques.

Species-Sorting and Niche Diversification

The *species-sorting paradigm* of metacommunity ecology suggests that habitat patches differ and will ultimately dictate regional community composition, and that species can coexist by means of niche diversification and differences in resource exploitation (Leibold et al. 2004). Food availability, physiological constraints, competition, and/or predation could be means which habitat partitioning occurs for reptiles (Toft 1985). Multiple lines of evidence indicate habitat partitioning by reptiles across prairie patch types (Fig. 2, Online Resource 6). Reptile richness was greatest in the Fire, F+G, and Legacy patches (despite an overall decrease in patch occupancy), and small-bodied snakes and lizards dominated richness. Within burned and heavily grazed grasslands, large reptiles are more vulnerable to predation (Wilgers and Horne 2007), so these small-bodied reptiles could be “fugitive species,” which disperse to take advantage of newly burned habitats to avoid predators or superior competitors (Hutchinson 1959). Alternatively, disturbance and dispersal may lessen the need to summon the competitive exclusion principle (Hardin 1960; Leibold et al. 2004). Although these data fit the *species-sorting paradigm* well, it is difficult to disentangle community assembly mechanisms and there may be a combination of processes and paradigms affecting these grassland herpetofauna (Logue et al. 2011).

Interestingly, no taxonomic order selected specifically for Control patches (Fig. 2). This result could be misconstrued as Control patches are unnecessary in the landscape;

however, reducing the total number of patches and types can decrease rates of population growth for organisms (Mittelbach 2012). Despite herpetofauna did not select the controls during spring sampling, these patches may still be important features for population regulation and community assemblage at other times of year. Further, these unburned and ungrazed patches could be refuges from fire or sources for recolonization.

Distribution and Dispersal Due to Land Management

Amphibian occupancy and dispersal probabilities did not change in response to treatments. In general, amphibians are poor dispersers and demonstrate site loyalty (e.g., Oldham 1966; Duellman and Trueb 1994; Blaustein et al. 1994; BeeBee 1996), and therefore likely operate as metapopulations (Harrison 1991; Marsh and Trenham 2001). For example, the American Toad (*B. americanus*) possesses homing capabilities and will navigate to the same breeding pool annually, even when other breeding sites are available (Oldham 1966). In this study, adult amphibians were closely associated with a particular watershed irrespective of treatment (Fig. 3), which is evidence of site fidelity and lack of dispersal. However, to fully understand site fidelity and dispersal dynamics, future study would need to uniquely mark and recapture individuals. Tadpole distribution is dependent upon where adults choose to place the eggs because tadpoles are restricted to water and likely have limited dispersal. The evidence of site fidelity and restricted tadpole movement may explain why amphibian community structure did not differ with land use.

Although I did not find direct amphibian responses, this does not preclude the possibility of negative consequences not measured here. Although prairie burning does not alter basic water chemistry (Larson et al. 2013a, b), the presence of cattle in riparian zones did. The cattle increased sediments and ammonium concentrations, which can be detrimental to tadpole development (Rouse et al. 1999; Schmutzer et al. 2008). Further, cattle trampling can widen stream channels (Belsky et al. 1999), which would reduce water depth and could cause stream drying prior to metamorphosis. Fully understanding the consequences of fire and cattle grazing on amphibians will require additional experimental manipulations and longer-term field studies (Pechmann et al. 1991).

Reptile occupancy (ψ) decreased and local extinction (ε) increased following the application of fire and grazing, and plausible mechanisms include mortality and/or behavioral avoidance by dispersal. Fire can cause direct mortality if animals are not able to escape or find refuge (Russell et al. 1999), and I documented burned reptile carcasses that could have affected ψ and ε estimates. Both fire and grazing decreased vegetative cover (Online Resource 4),

which can make large reptiles more vulnerable to predation (Wilgers and Horne 2007).

Recolonization (γ) for reptiles was a low rate of <10 % and marginally increased with time across all patch types. This simply could be that animal activity was increasing through the primary seasons (March–June). Interpretation of γ should be cautioned because it is a limited estimate of dispersal according to the narrow definition (an unoccupied patch in time t becomes occupied in time $t + 1$). Therefore, colonization in an already occupied patch would not be detected.

A future challenge for ecologists is obtaining accurate estimates of dispersal (Jacobson and Peres-Neto 2010). Metacommunities are perplexing because the community is comprised of multiple species with different dispersal capabilities and behaviors (Smith and Green 2005), for which we are often data deficient. Further, metacommunities operate within a landscape context where dispersal may be limited by patch size and distance between patches (Smith and Green 2005). Current dispersal estimates, such as local extinction probabilities (ε), do not capture the mechanism(s) of extinction. For example, this occupancy analysis detected changes in reptile occupancy and extinction following fire and grazing, yet cannot determine whether this is due to mortality, dispersal, or both. This occupancy analysis showed that reptiles responded to land management and thus warrants future studies of species dispersal capacity and the underlying mechanism(s), as well as spatially explicit models to incorporate landscape metrics like patch size and configuration.

Management Implications

Successful grassland conservation requires understanding the effects of disturbance and landscape heterogeneity. Fire and grazing are natural and essential ecosystem processes in grasslands, and therefore will be continued. However, the majority of remaining tallgrass prairie is currently managed by annual prescribed burning and high-density grazing in large landscape patches (Derner et al. 2006) which does not mimic the historical patterns or co-evolution with herpetofauna.

Several studies suggest PBG is feasible and has benefits to plants and wildlife across many grassland types. PBG may be a viable and attractive option for livestock farmers because the practice does not hinder cattle weights (Limb et al. 2011), and can reduce cattle pests (Scasta et al. 2012) and invasive plant species (Cummings et al. 2007). Further, previous studies showed PBG had positive effects on birds (Fuhlendorf et al. 2006), small mammals (Fuhlendorf et al. 2010), and insects (Engle et al. 2008). In this study, reptiles selected for a variety of burning and grazing conditions, which provides support for the PBG design in

terms of increasing reptile richness at the patch scale. Consequently, the conservation of grassland herpetofauna requires an array of patch types that include fire and grazing.

Acknowledgments I thank the Missouri Department of Conservation and the Columbus Zoo for funding. K. Sullivan and L. Gilmore were key players in the burning and grazing execution of this study. I especially thank all my fellow froggers for field assistance: T. Laszkowski, T. Thompson, S. Whittaker, C. Larson, J. Maine, W. Dodds, and L. Banschach. Valuable manuscript comments were provided by B. Sandercock, K. Gido, J. Whitney, W. Dodds, M. Daniels, M. Whiles, M. Troia, J. Perkin, and three anonymous reviewers. This research was conducted under the IACUC protocol (#2953) and the Missouri State Wildlife Collection Permits (#SC-137-2010, #SC-001-2011, #15084).

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