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FIELD NOTE

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Midwest prairie management practices benefit the non-target prairie crayfish

Caitlin C. Bloomer[1*], Christopher M. Miller[1], Robert J. DiStefano[2] and Christopher A. Taylor[1]

Abstract

Background Prescribed burning is used to duplicate natural, pre-settlement prairie successional processes. It is an essential and commonly used tool to promote and protect biodiversity and enhance ecosystem function in tallgrass prairie remnants throughout the midwestern United States. The responses to prescribed burns vary widely among faunal groups. We conducted the first study into the response of the prairie crayfish (*Procambarus gracilis* Bundy) to periodic prescribed burns and other management activities in a tallgrass prairie in Northern Missouri. This species relies on natural and restored prairies across its broad distribution, but little is known on how to actively manage these populations.

Results We found that the density of the prairie crayfish burrows did not vary in response to the burn regime; however, other management activities like the installation of artificial ponds for amphibians and reptiles were directly benefitting this species. Observations indicate that prairie crayfish may also show positive associations with warm-season grass stands and vegetation management should be further explored.

Conclusions The current prairie management practices for vegetation, quail, and herpetofauna are having beneficial or neutral effects on non-target taxa like the prairie crayfish. The value of crayfish and their burrows in prairies is well-established. Conservation biologists should continue to examine how burrowing crayfish are responding to management practices for other taxa to explicitly manage and promote these populations.

Keywords Burrowing crayfish, Missouri, Prescribed burn, Fire, Ponds, Prairie management

Resumen

Antecedentes Las quemas prescriptas son usadas para duplicar los procesos sucesionales naturales que ocurrían en las praderas de los EEUU previo al proceso de colonización. Estas quemas representan una herramienta esencial y comúnmente usada para promover y proteger la biodiversidad, y aumentar las funciones del ecosistema en los remanentes de las praderas de pastos altos (tallgrass prairie) en el medio-oeste de los estados Unidos. Las respuestas a las quemas prescriptas varían ampliamente entre los grupos de fauna de esas praderas. Condujimos el primer estudio sobre las respuestas del cangrejo de las praderas (Procambarus gracilis Bundy) a las quemas prescriptas y otras actividades de manejo en una pradera de pastos altos del norte de Missouri. Esta especie (cangrejo de las praderas) habita en toda la amplia distribución de praderas naturales y restauradas, aunque se conoce muy poco sobre cómo manejar activamente sus poblaciones.

Resultados Encontramos que la densidad de las cuevas de los cangrejos de las praderas no varía en relación al régimen de quemas. Sin embargo, otras actividades de manejo como la instalación de charcas artificiales para anfibios

*Correspondence:
Caitlin C. Bloomer
bloomer3@illinois.edu
Full list of author information is available at the end of the article

y reptiles benefician directamente a esta especie. Las observaciones indican que el cangrejo de las praderas puede asimismo mostrar asociaciones positivas con comunidades de pastos de estación cálida, por lo que el manejo de la vegetación debería ser también explorado.

Conclusiones Las practicas corrientes de manejo de la vegetación, de las codornices, y de la herpetofauna, están mostrando efectos beneficiosos o tal vez neutros en taxones no prominentes como el cangrejo de las praderas. El valor de los cangrejos de las praderas y sus cuevas han sido bien ponderados. Los biólogos de la conservación deben continuar examinando cómo los cangrejos excavadores están respondiendo a las prácticas de manejo para otros taxones, para explícitamente manejar y promover sus poblaciones.

Background

Northern Missouri, like much of the midwestern United States (U.S.), was once dominated by tallgrass prairies. Over 95% of tallgrass prairies have been lost to agriculture, urbanization, and fire suppression (Smith 2001), so these prairie remnants are carefully stewarded by conservation managers and government agencies. Fire is a powerful agent of natural disturbance and prescribed burns are a common management tool across the midwestern U.S. to maintain healthy prairies (Collins and Wallace 1990). While having a dramatic immediate impact, prescribed burns can also improve long-term nutrient cycling, promote the growth of native grasses and forbs, and maintain the ecosystem structure of prairies. These ecosystems rely on periodic burning to maintain both flora and fauna community compositions and prevent late-stage succession, supporting a more dynamic environment (Pausas & Keeley 2009).

Some terrestrial invertebrate communities can be negatively impacted by prescribed burns (Panzer 2002; Tooker & Hanks 2004). Slower-moving invertebrates like molluscs demonstrate lower abundance and diversity in burned prairies compared to unburned prairies (Severns 2005). Fire-adapted invertebrates, however, may display fire-negative responses during the initial burn, but quickly recolonize the area within months (Reed 1997; Harper et al. 2000). Further, subterranean arthropods and aquatic invertebrates in prairie streams can tolerate prescribed burns and can benefit from the increased ecosystem productivity (Lussenhop 1976; Fulgoni et al. 2020). A subterranean group of macroinvertebrates, burrowing crayfish, often inhabit prairies (Welch et al. 2008; Bearden et al. 2022) yet their response to prescribed burns has not been documented.

Several species of burrowing crayfish are known to inhabit prairies including the Jackson prairie crayfish (*Procambarus barbiger* Fitzpatrick), the southeastern prairie crayfish (*P. hagenianus* Faxon), and most widespread, the prairie crayfish (*P. gracilis* Bundy). Burrowing crayfish are fossorial, creating deep and complex burrows to the groundwater where they will spend most of their life (Hobbs 1942). Their specialized habitats bridge the gap between terrestrial and aquatic environments making their responses to prairie management unpredictable. Burrowing crayfish species have responded positively to anthropogenic disturbance, including burning and disking, in some wetland ecosystems with their presence correlated with the associated post-disturbance vegetation composition (Adams et al. 2021; Bloomer et al. 2022). In prairies, crayfish burrows provide vital refuge for insects and herpetofauna seeking protection during prescribed burns (Russell et al. 1999; Baecher et al. 2018). Burrow excavation facilitates soil nutrient turnover, soil aeration, and subsurface water flow which can promote native plant communities (Richardson 1983). In addition, their semi-terrestrial lifestyle allows them to serve as a prey resource for birds and mammals (Hobbs 1993). Despite their established value in prairie ecosystems, there is little guidance for conservation managers on how to manage for or promote burrowing crayfish populations.

The aim of this study was to provide the first insight into the response of the widespread prairie crayfish (Fig. 1) to prescribed burning in a tallgrass prairie ecosystem. We measured the density of active prairie crayfish burrows in fields undergoing periodic burning regimes to study the effect of short-term fire suppression on crayfish. We hypothesized that “years since prescribed burn” would have no effect on short-term crayfish burrow presence for two reasons; because the prairie crayfish

Fig. 1 A Form I Male *Procambarus gracilis* collected from Sears Memorial Wildlife Area in Audrain County, Missouri. Photo courtesy of Dusty Swedberg

inhabits subterranean habitats in grasslands, we did not expect to see a negative response to burning practices. Secondly, the species also occupies wetlands and forested areas, so we also did not expect recently burned prairies to be a preferred habitat. By developing a quantitative understanding of crayfish response to prescribed burns, we hope that conservation managers can more explicitly promote crayfish populations in their management plans.

Methods

Study site

This study was conducted at the F.O. and Leda J. Sears Memorial Wildlife Area in Audrain County, Missouri (Fig. 2). This 65-ha area is managed by the Missouri Department of Conservation for prairie grasses and seasonal wetlands. It is closed to hunting, and experiences only light public use. It is a hydric area, with little topographic relief for drainage, making it suitable habitat for burrowing crayfish. Native vegetation has been established here since the mid-1990s and it is currently managed with controlled burns only. The area contains six permanent 0.2-ha ponds, installed for amphibian breeding habitat.

The conservation area is divided into 16-ha quarters, of which we selected three for this study. Our selected quarters were burned on rotation with one quarter burned in each of Spring 2019, 2020, and 2021. The quarter burned in Spring 2019 was burned again in Spring 2022. Prior to this study, quarters were burned sporadically with an average of 3 years between burns. We sampled for burrowing crayfish populations post-burn in April 2021 and April 2022 (Fig. 2).

Field sampling

A 340×340 m area was delineated within each 16-ha field, covering most of the available space. A 10-m buffer from the outer limits of the field was maintained, to avoid edge effects from vehicles or mowing. Fifty sampling sites per quarter were selected a priori using randomly generated XY points, which were identified on site using a rangefinder and compass. A 1-m^2 white PVC quadrat was placed at each sampling site. A GPS coordinate was recorded at the bottom left corner of each quadrat. The quadrat was searched, the presence of active burrows found within the quadrat was recorded as our response variable, and each burrow was carefully excavated to capture crayfish within it. Active burrows were defined as any burrow with fresh mud at the entrance, a substantial chimney, or a smooth, circular entrance hole that was not obstructed with grass or debris (e.g., Fig. 3). Any crayfish captured were identified and sexed in the field. Four representative specimens were retained and

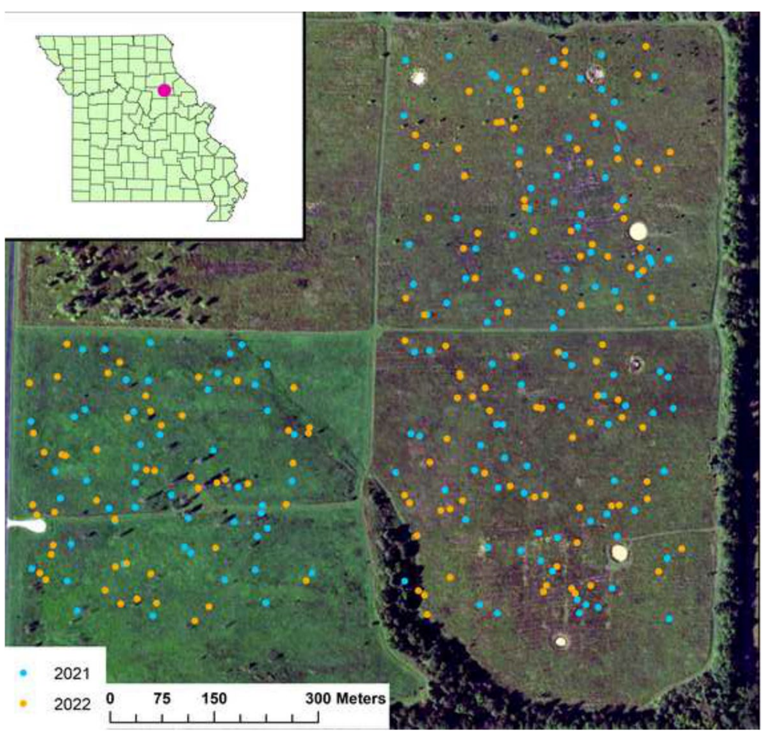

Fig. 2 An aerial image of Sears Memorial Wildlife Area in Audrain County, Missouri. Randomized sampling points are color-coded by sampling year across the three periodically burned sites. Six circular ponds are visible on the eastern half of the area

Fig. 3 Two examples of active *Procambarus gracilis* burrow entrances at the base of recently burned warm-season grass stands

vouchered in the Illinois Natural History Survey Crustacean Collection.

During our 2022 field sampling, fifty new quadrat locations per quarter were randomly selected. We visually assessed and recorded the common prairie vegetation within the conservation area. Additional habitat data was recorded using ArcMap layers. Elevation was recorded from LiDAR data hosted by the Missouri Spatial Data Information Service (MSDIS). Soil organic carbon up to a depth of 150 m was recorded from Gridded Soil Survey Geographic (gSSURGO) hosted by the U. S. Department of Agriculture (USDA). We delineated the artificial 0.2-ha ponds in the fields and calculated Euclidean distance to the edge of the nearest pond (m) in ArcMap. We also calculated Euclidean distance to West Lick Creek, a natural stream along the perimeter of the property, in ArcMap.

Statistical analysis

We then used two suites of generalized linear mixed-effects models (GLMMs) to examine relationships between crayfish burrow presence or density and selected habitat variables. The response variable in each model was the presence-absence or density of active burrows recorded within each 1 m^2 quadrat. Habitat variables for this analysis included the number of years since burning, elevation (m), soil organic carbon (%), Euclidean distances to artificial ponds (m), and Euclidean distance to a natural stream (m). The habitat variables were centered and scaled prior to analysis. Spearman's correlation coefficient (ρ) was used to test for multicollinearity in habitat variables. Statistical analyses were conducted in R (version 4.3.1, R Core Development Team 2017), and candidate models were fit using R package glmmTMB (version 1.1.8; Brooks et al. 2017). The response was modeled with a Binomial distribution with a log link for burrow presence and a Poisson distribution for burrow density. The land surrounding our study site is agricultural and did not provide an unburned, undisturbed area that could act as a control for our study. Therefore, we modeled our data as the response to years since burning within the site.

To determine if there was a temporal effect from sampling over 2 years, we first ran an analysis of variance (ANOVA) on mean burrow presence between 2021 and 2022. The sampling year and the variable "years since burning" were confounded so sampling year was not included in our GLMMs as a fixed effect. To account for spatial autocorrelation within our experimental design, we included a nested random effect of quadrat within quarter and used an unstructured covariance matrix.

For our two response variables of burrow presence and density, global models containing all predictor variables and null models were fitted. The marginal r^2 and overdispersion parameter c-hat were used to assess the fit of the global models. Ten candidate models for each response variable were developed and evaluated using Akaike's Information Criterion with a small sample size correction (AICc; Akaike 1974). The top models were defined as having ΔAICc values < 2.0 and containing majority weight when combined. Model selection and averaging was conducted through the R package MuMIn (Barton 2014). The top models were averaged and used to assess significance at $\alpha = 0.05$. Model-averaged parameter estimates were used to predict burrowing crayfish density for each predictor variable.

Results

We recorded 82 active burrows, with 10 individual crayfish captured across the two sampling periods. All crayfish collected were identified as prairie crayfish and we assumed that all active burrows recorded were inhabited by this species. There was no significant difference in mean burrow presence between 2021 and 2022 ($p = 0.786$) so the data were not subset by year for modeling.

When evaluating burrow presence, the global model for our variables ranked below the null model, indicating that some of our variables were not good predictors of crayfish presence. Three top models were averaged to form the final model for habitat variables (Table 1). Euclidean distance to artificial ponds, elevation, and soil organic carbon content were all significant predictors of crayfish presence ($p < 0.05$; Table 2).

When evaluating burrow density, two top models were averaged to form the final model, including the same three predictor variables as the final model for burrow presence (Table 2). Euclidean distance from the pond was negatively correlated with burrow presence and density, whereas soil organic carbon and elevation were positively correlated (Fig. 4). The number of years since burning nor distance to the nearest natural waterbody was not included in either of the final models.

Table 1 Generalized linear mixed model results for prairie crayfish burrow presence and density in a tallgrass prairie in Missouri. The null model, global model, and top models that were averaged to produce the final models are presented with difference in AIC (ΔAIC), Akaike weight (Wi), and log likelihood (LL). All models included a nested random effect for quadrat within burned quarter of the conservation area

Model variables	AICc	ΔAICc	Wi	LL
Burrow presence				
Elevation + distance to artificial pond	326.5	0.00	0.512	− 158.17
Soil organic carbon	327.7	1.16	0.286	− 159.78
Elevation + distance to artificial pond + years since burning	330.4	3.88	0.074	− 158.01
Null model	332.0	5.51	0.033	− 162.98
Global model	333.5	6.99	0.016	− 157.45
Burrow density				
Elevation + distance to artificial pond	391.8	0.00	0.397	− 190.82
Soil organic carbon	392.0	0.21	0.356	− 191.96
Null model	398.2	6.41	0.016	− 196.08
Global model	397.0	5.20	0.029	− 189.21

Observations

This study yielded some surprising observations. The vegetation assemblage of the study area was early-successional, dominated by warm-season grasses and forbs. Cool-season grasses and incidental shrubs were present throughout the study area. Warm-season grass stands consisted of little bluestem (*Schizachyrium* spp.), big bluestem (*Andropogon gerardii* Vitman), indiangrass (*Sorghastrum* spp.), and switchgrass (*Panicum virgatum* L.). Cool-season grass stands consisted of Kentucky bluegrass (*Poa pratensis* L.), fescue (*Festuca* spp.), smooth brome (*Bromus inermis* Leyss.), and reed canary grass (*Phalaris arundinacea* L.). Other frequently recorded plants included goldenrod (*Solidago* spp.), milkweed (*Asclepias* spp.), wild white indigo (*Baptisia alba* Vent), indianhemp (*Apocynum cannabinum* L.), and multiflora rose (*Rosa multiflora* Thunb). A potential positive association between warm-season grass stands and active crayfish burrows was observed (e.g., Fig. 3). While we did not collect adequate data to statistically assess this trend, we considered it prominent enough to report in this study.

Additionally, we observed that, in excavated burrows, the entrance tunnels to chambers often extended beyond 1 m depth and we frequently could not reach the end of a burrow. The deepest excavation we undertook extended approximately 2 m into the ground which was deeper

Table 2 Model averaged parameter estimates of the top models for prairie crayfish burrow presence and density in a tallgrass prairie in Missouri. Bold values indicate significant results at $\alpha = 0.05$

Variable	Model averaged estimate (SE)	95% confidence limits	$P > \|z\|$
Burrow presence			
Distance to artificial ponds	− 2.016 (0.685)	− 3.364, − 0.668	**0.003**
Elevation	0.850 (0.271)	0.316, 1.384	**0.002**
Soil organic carbon content	0.334 (0.131)	0.076, 0.592	**0.011**
Burrow density			
Distance to artificial ponds	− 1.782 (0.534)	− 2.834, − 0.731	**0.001**
Elevation	0.753 (0.214)	0.332, 1.173	**0.001**
Soil organic carbon content	0.324 (0.109)	0.110, 0.537	**0.003**

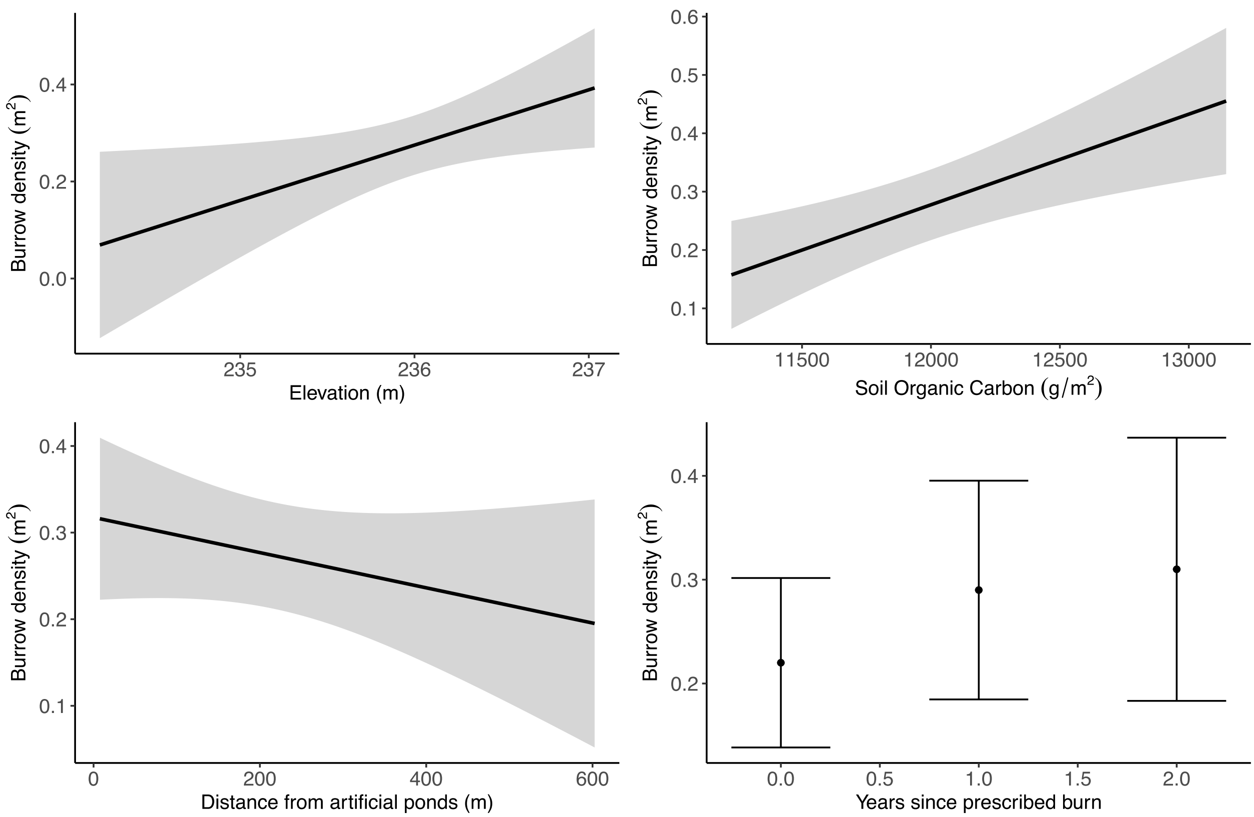

Fig. 4 Crayfish burrow density by habitat variables with 95% confidence intervals. Elevation, soil organic carbon and distance from artificial ponds were significant predictors of burrow density at $\alpha = 0.05$

than expected given our experience excavating this species from roadside ditches in Missouri.

Discussion

Prairie crayfish did not exhibit a short-term response to the prescribed burning in this tallgrass prairie. In our relatively small study area, movement between burned and unburned sites should have been possible, yet no difference in crayfish presence or density was recorded. Given that fire in prairies was commonly induced by weather or Native American practices before European colonization, it is likely that prairie crayfish were pre-adapted to prescribed burns. This species appears tolerant of prescribed burns, and it may even benefit from the results of these burns such as the increased root biomass and warm-season grass stands which can serve as food sources (Kucera et al. 1967; Hulbert 1986). Agricultural practice, urban expansion, and the exclusion of fire have led to loss of prairie habitat and the decline of many species (Samson et al. 2004). From our study and previous literature (Hobbs and Rewolinski 1985), we believe that prairie crayfish would be similarly disadvantaged by the loss of prairies.

Hydrologic variation in prairies, and their associated seasonal wetlands, produces heterogeneous soils and diverse habitat structure which in turn promotes biological diversity (Baecher et al. 2018). Restoring or creating aquatic (fishless) habitat is critical to support breeding of prairie herpetofauna. The artificial ponds in our study area were installed by Missouri Department of Conservation to provide reptile and amphibian breeding habitat. An unexpected result from our study was the significance of proximity to artificial ponds, but the non-significance of proximity to the natural stream to burrow presence and density. We hypothesize that the distribution of prairie crayfish in our study area may be driven by fine-scale groundwater depth and moisture regimes (Bearden et al. 2022). This distributional trend is displayed by some amphibians which show increased resilience to fire through their burrowing behavior (Friend 1993). Further, hydrologic prairie restoration has been shown to benefit species such as Graham's crayfish snake (*Regina grahamii*, Baird & Girard) which rely on crayfish as a primary food source, and the crawfish frog (*Lithobates areolatus*, Baird & Girard) which rely on crayfish burrows for habitat (Baecher et al. 2018). The management practice of installing artificial ponds serves to benefit both the target herpetofauna and the crayfish these taxa rely on.

Elevation and soil organic carbon also had significant effects on the distribution of prairie crayfish across the prairie. We used LiDAR elevation data to measure finer-scale differences in elevation within our site and found an increased presence of burrows on slightly elevated areas of the prairie. This further indicates that prairie crayfish are influenced by fine-scale habitat variables within a site such as moisture regimes. Other burrowing species avoid frequently flooded areas in favor of seasonally flooded areas (Bloomer et al. 2022). Prairie crayfish may choose slightly elevated habitats to avoid long periods of inundation. Similarly, prairie crayfish showed a positive association with soil organic carbon which is an indicator of nutrient retention, soil structure, and moisture retention (Carter 1995). Our soil data was measured from gSSURGO on a 30 × 30 m grain, supporting our hypothesis that fine-scale habitat variables can influence the distribution of crayfish within a site. These habitat variables likely serve as analogs for the fine-scale moisture regime or food availability via plant density.

We present some notable observations from our field study which, while we did not collect sufficient data to statistically analyze, are reported here to inform future field studies. First, we noted the association of crayfish burrows with warm-season grass stands which was repeatedly observed throughout the study site. We propose two biological explanations for this purported association. Warm-season grass stands increase soil stability and water infiltration (Paredes et al. 2018) which may support burrow construction or crayfish may rely on increased root biomass as a food source (Graham et al. 2022). Additionally, the bunchgrass growth habit of several warm-season grass species creates interspaces of bare soil in their stands. These interspaces facilitate overland movement of wildlife and provide protection from visual predators. Ground-nesting birds such as quail are known to use these interspaces, and we propose that prairie crayfish might do the same. Promoting warm-season grass stands is a common grassland management practice in governmental schemes such as the Conservation Reserve Program to promote quail populations (Washburn et al. 2000). Future research into the fine-scale vegetation associations of prairie crayfish and other burrowing crayfish may corroborate that these practices are also benefiting non-target taxa.

Our second observation was the increased depth of burrows compared to roadside ditch sites where we have collected this species. Crayfish burrows have been reported with mean depths around 1 m or less (Johnston & Figiel 1997; Dorn & Trexler 2007; Welch et al. 2008). Several burrows excavated in the burned prairie presented with initial tunnels to the main chambers deeper than 1 m, and often could not be excavated to the bottom. As soil temperature is higher in burned prairie plots (Hulbert 1986), our observations suggest that prairie crayfish use deeper burrows to tolerate the increased temperature and other surface impacts of fire.

Conclusions

Prairie ecosystems serve as a primary habitat for the prairie crayfish across its extensive range. Encroachment on these ecosystems from agriculture and urbanization was noted as a key concern for the conservation of this species several decades ago (Hobbs and Rewolinski 1985). Roadside ditches serve as remnant prairie habitats (Davis et al., 2007) which support the persistence of burrowing crayfish populations despite the loss of true prairie habitat. Primary burrowing crayfish provide critical services to prairie ecosystems as a prey source and through the construction of their burrows. We have previously highlighted examples of management practices that benefit both target taxa and non-target crayfish (Bloomer et al. 2022). This study highlighted that prairie crayfish are among the fire-adapted invertebrates that appear tolerant of prescribed burns. In our study, they benefitted from other prairie management practices including the installation of artificial ponds and potentially the promotion of warm season grass stands. These practices are implemented to support specific taxa, like quail and herpetofauna, but have broader implications for non-target taxa as well. This is a positive result for the prairie crayfish; however, given the drastic historical loss of prairies, conservation managers should strive to explicitly manage for burrowing crayfish in prairie management plans to ensure their continued protection.

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Authors' contributions
CAT, RJD, and CCB contributed to the conception and design of the work. CCB and CMM led the data collection. CCB led the data analysis. All authors contributed to the interpretation of the data and drafting of the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials
The specimens collected during this study are cataloged in the Illinois Natural History Survey Crustacean Collection. The datasets generated during this study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

Author details
[1]Illinois Natural History Survey, Prairie Research Institute, 1816 S. Oak St, Champaign, IL 61820, USA. [2]Missouri Department of Conservation, 3500 E Gans Road, Columbia, MO 65201, USA.

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