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Integrating burrowing crayfish and waterfowl conservation management on moist-soil wetlands

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Summary

The North American Waterfowl Management Plan highlights the importance of enhancing waterfowl habitat for productivity and resilience. Many forms of land management are conducted in wetlands to support the diverse communities of waterfowl and other species. Primary burrowing crayfish are also abundant and important in these environments, but little research is available assessing the effects of waterfowl land management on primary burrowers. We examined the response of the digger crayfish, *Creaserinus fodiens*, to the common vegetation management practices of mowing and disking at waterfowl conservation areas in southeastern Missouri. Our results demonstrated that at a fine scale, crayfish density was affected by only canopy cover. We also highlighted distributional effects of landscape-level environmental variables and suggested that habitat generalists were tolerant of vegetation management, responding more to vegetation composition and broader landscape effects. We discuss wetlands conservation practices and suggest that burrowing crayfish management would integrate well with some current management strategies for waterfowl.

Introduction

Burrowing crayfish populate most aquatic and semi-aquatic habitats in North America, including swamps, floodplain forests and prairies (Abell et al. 2000). They provide important ecosystem functions including soil mixing and aeration (Richardson 1983, Stone 1993), habitat provision (Williams et al. 1974, Pintor & Soluk 2006) and serving key trophic roles (Hobbs 1993). However, the paucity of data on these organisms is well established (Moore et al. 2013, Bloomer et al. 2021). There are often not enough distribution or natural history data on burrowing crayfish to inform spatial patterns or direct surveys (Welch & Eversole 2006). Habitat loss through land-use change has been highlighted as a specific conservation concern (Taylor et al. 2019). To improve the success of conservation measures for burrowing species it is important to understand habitat associations and responses to land management activities (Moore et al. 2013).

Many land management practices are employed across private agricultural land, publicly owned properties and private easements (Oudenhoven et al. 2012), including prescribed burns, mechanical vegetation disturbance, hydrologic manipulation and chemical treatment. On moist-soil wetlands in the USA, management efforts focus on vegetation and hydrologic regimes (Fredrickson 1991, de Szalay 1997). Negative impacts of land management practices are documented for aquatic invertebrates and fish (e.g., Berkman et al. 1986, Wrubleski & Ross 2011) but little focus has been placed on burrowing crayfish.

Mowing is perhaps the most common land management practice employed on the terrestrial landscape. Plant diversity and nutrient cycling in agricultural grasslands benefit from semi-frequent cutting (Antonsen & Olsson 2005). Mowing has mixed effects on macroinvertebrates (Szalay & Resh 1997, Humbert et al. 2010). The direct effects on burrowing crayfish have not been investigated; however, mowed roadside ditches are frequently inhabited (Tack 1941, Rhoden et al. 2016).

Disking is another commonly employed activity for managed landscapes and is used to break up soil, chop stover from previous agricultural crops and mix topsoil layers, often enhancing soil organic material (Komatsuzaki & Ohta 2007). Spring or early summer disking is the most common mechanical manipulation practice used in wetlands (Gray et al. 2013). This practice hinders succession, impeding the emergence of woody vegetation and promoting a higher diversity of seed-producing plants for wetland birds during autumn migration periods (Missouri Department of Conservation 2009). The effects of disking have only been examined in *Procambarus clarkii*, usually classed as a secondary or tertiary burrower. The results were conflicting, with both negative and positive responses to disking (Chien & Avault 1983, Gray et al.

1999). However, it was noted that disking increases aeration and loosens soil (Gray et al. 1999), potentially reducing the energetic costs of excavating soil.

We examined how vegetation management might affect burrowing crayfish at two Missouri Department of Conservation (MDC)-owned conservation areas that are managed for waterfowl. Our study objectives were to: (1) identify the fine-scale and landscape-level characteristics of primary burrowing crayfish habitat; and (2) determine the response of burrowing crayfish to mowing and disking on these public properties.

Methods

Study areas

The Mississippi Alluvial Valley contains rich, moist soils suitable for burrowing crayfish. We identified two publicly owned properties in south-eastern Missouri – Duck Creek and Otter Slough Conservation Areas – with similar management practices and known crayfish presence. Both properties lie in the Pleistocene Valley Trains ecoregion. They are moist-soil wetlands managed by MDC for resident and migratory waterfowl and other wildlife. Ephemeral wetlands on site are disked annually during the dry season to promote native plant growth. Roadside ditches, levees and trails are mowed biannually for access. Unmanaged land on the properties often presents as units of native, bottomland forest that are maintained for wildlife habitat and food supplies of acorns and invertebrates.

Environmental data and sampling

Sampling was conducted in spring 2021. At each property, 11 40m transects were established in each of the three management types: disked, mowed and unmanaged. Transects were placed randomly with a minimum of 100 m spacing to ensure independence. Each transect had five 1m^2 polyvinyl chloride (PVC) quadrats placed at 10 m intervals.

Within each quadrat we measured percentage of tree canopy cover, percentage of herbaceous ground cover, presence/absence of hydrophilic sedges, presence/absence of surface water, stem density and number of active burrows (see below). Canopy cover was estimated using a concave spherical densiometer (model C; Robert E. Lemmon, Forest Densiometers, Bartlesville, OK, USA) and inverted for herbaceous ground cover (Rhoden et al. 2016). Stem density was measured using a 10cm^2 quadrat placed in the upper left-hand corner of each 1m^2 quadrat. A soil sample was collected at the third quadrat of each transect using a soil probe (AMS ⅞ in. open-end probe; AMS, American Falls, ID, USA) to an approximate depth of 50 cm. Soil samples were analysed for percentage composition (sand, silt and clay) by laser diffraction using a Malvern Mastersizer 3000 (Malvern Instruments, Malvern, UK). Selected habitat variables have previously been associated with other burrowing crayfish species in the south-eastern USA (Welch & Eversole 2006, Rhoden et al. 2016). As only one soil sample was analysed, habitat variables across the quadrats were averaged to provide one measurement per transect. All active burrows within the quadrats were counted and burrow counts were averaged over transects to provide density as burrows/m^2.

Active burrows were defined as burrows with freshly excavated mud at the entrances, substantial chimneys or smooth-walled entrances with no vegetation growth or debris in the opening (Helms et al. 2013). All active burrows that fell within quadrats were excavated by hand. Crayfish captured were taxonomically identified and sexed, with representative specimens vouchered in the Illinois Natural History Survey Crustacean Collection.

The landscape-level environmental variables selected were elevation, available soil water storage up to 1.5 m depth, Euclidean distance to the nearest stream and average annual precipitation. Elevation was measured from the United States Geological Survey digital elevation map. Available soil water storage was measured from the United States Department of Agriculture gridded soil survey geographic database. Euclidean distance was calculated in *ArcGIS* using the National Hydrography Dataset. Average annual precipitation was measured from the PRISM Climate Group data from Oregon State University (http://prism.oregonstate.edu).

Statistical analysis

We used generalized linear mixed models (GLMMs) to examine relationships between burrow density and fine-scale habitat variables. Statistical analyses were conducted using *R* version 3.3.2 (R Core Development Team 2017). The predictor habitat variables were centred and scaled prior to analysis. Spearman's correlation coefficient (ρs) was used to test for multicollinearity in predictor variables. Stem density, herbaceous ground cover and canopy cover were significantly correlated ($\rho s \geq 0.60$); therefore, only canopy cover was included in the fine-scale models. Models were zero-inflated to account for low detection. Candidate models were fitted using the *R* package *glmmADMB* (Fournier et al. 2012). Burrow density was modelled with a zero-inflated Poisson distribution with a log-link. Conservation area was included as a random effect in models to account for potential effects from using two separate properties. A global model containing selected predictor variables and conservation area as a random effect was fitted. The marginal r^2 and overdispersion parameter c-hat were used to assess the fit of the models. Candidate models were evaluated using Akaike's information criterion (AIC) with a small sample size correction (AIC_c; Akaike 1974). The top model(s) were defined as having ΔAIC_c values < 2.0 and containing majority weight (Burnham & Anderson 2002). Model selection was conducted through the *R* package *MuMIn* (Barton 2014). Variables in the top model were assessed for significance at $\alpha = 0.05$.

We used a second set of GLMMs to examine the relationships between burrow presence and landscape-level environmental variables. The response variable was active burrow presence or absence within a transect. Using GLMMs, the response variable was modelled with a binomial distribution with a log-link. As above, conservation area was included as a random effect and model fit was assessed with marginal r^2 and c-hat. The top models ($AIC_c < 2.5$; Table 1) were averaged using the *R* package *MuMIn* (Barton 2014) to contain a majority weight. Variables were assessed for significance at $\alpha = 0.05$.

Results

A total of 110 active burrows were recorded, with 30 individual crayfish captured in transects across the two properties. Twenty-six of the individuals collected were primary burrowing crayfish, *Creaserinus fodiens*. One individual each of *Procambarus viaeviridis* and *Lacunicambarus ludovicianus* was captured in mowed transects. As only one of each of these species was recovered and no other nearby burrows were recorded, they were excluded from statistical modelling. Two *Procambarus acutus* were collected from very shallow (<15cm), single-chamber burrows in transects.

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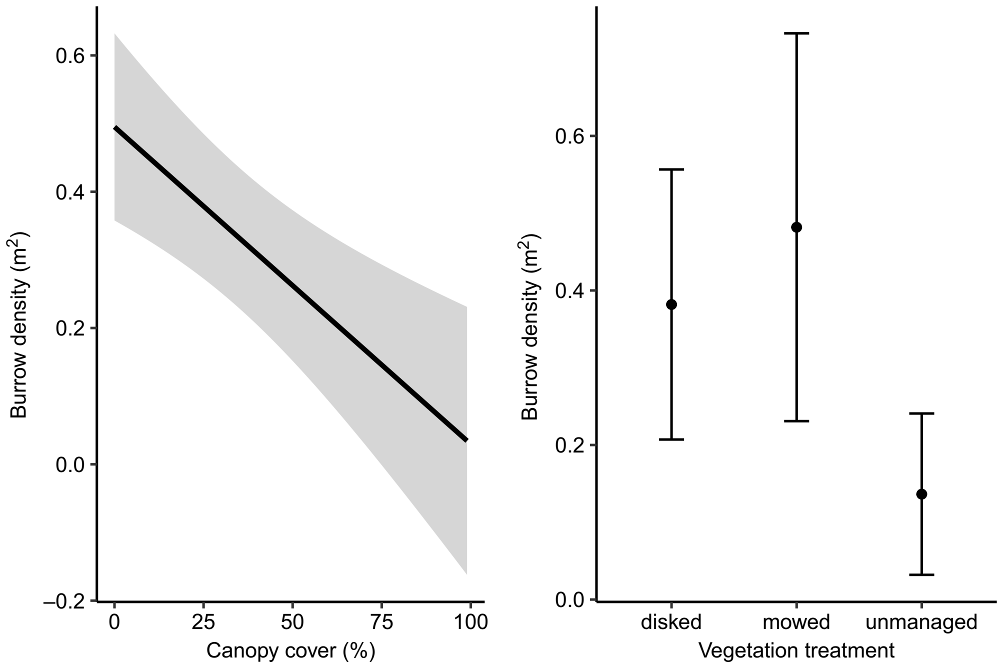

Fig. 1. Estimated number of *Creaserinus fodiens* burrows/m^2 (95% confidence intervals) in relation to percentage of canopy cover (significant) and vegetation management (not significant).

Table 1. Generalized linear mixed model results for *Creaserinus fodiens* density (active burrows/m^2) and fine-scale habitat data and *C. fodiens* burrow presence and landscape-level environmental data. The top five models, global model and null model for each are included. Models are ranked by Akaike's information criterion (AIC) with small sample size correction (AIC$_c$). Difference in AIC$_c$ (ΔAIC$_c$), Akaike weight (W_i),and log likelihood (LL) are presented. For fine-scale variables: canopy = canopy cover (%); sand = soil composition classed as sand (%); sedge = presence/absence of sedges; water = presence/absence of surface water; treatment = land management treatment (disked, mowed or unmanaged). For landscape-level variables: AWS = available water storage in the first 150 cm of soil; Precip = average annual precipitation (cm); EucStr = Euclidean distance to nearest stream (m); Elev = elevation (m). Data were collected from two conservation areas in south-western Missouri

Model variables	AIC$_c$	ΔAIC$_c$	W_i	LL
Fine-scale habitat variables				
Canopy	91.1	0.00	0.777	−41.197
Treatment	96.6	5.59	0.046	−42.818
Null model	96.8	5.70	0.043	−45.183
Water	97.4	6.33	0.031	−44.361
Sand + treatment	98.3	7.23	0.020	−42.428
Sand	98.3	7.29	0.020	−44.840
Global model (all variables)	98.7	7.65	0.017	−38.742
Landscape-level environmental variables				
AWS + Precip + EucStr	71.3	0.00	0.377	−30.155
AWS + Precip	71.5	0.23	0.336	−31.443
Global model (All variables)	73.4	2.09	0.133	−29.987
AWS + Precip + Elev	73.5	2.23	0.124	−31.270
AWS + EucStr	77.6	6.32	0.016	−34.486
AWS	78.2	6.90	0.012	−35.912
Null model	95.3	23.95	0.000	−45.533

As this is a tertiary burrowing species, these individuals were also excluded. The remaining 106 active burrows were assumed to be *C. fodiens*. Additional excavated burrows and moulted exuviae outside the transects were also used to confirm the population species.

Only canopy cover was included in the top model for fine-scale environmental variables (Table 1). Canopy cover was a significant predictor ($p = 0.017$) of *C. fodiens* density, with lower canopy cover percentage being preferred (Fig. 1). Vegetation treatment was not present in the top model, nor was it significant in the global model ($p = 0.3$) of all fine-scale variables. The top model held a modest weight and several models ranked below the null model (Table 1). There was a non-significant decline in burrow density between the managed sites and the unmanaged sites (Fig. 1). Herbaceous ground cover and stem density were both excluded from modelling due to correlation with canopy cover. However, when canopy cover was removed and models run with herbaceous ground cover or stem density, neither was included in top models, nor was herbaceous ground cover or stem density significant in the global models (herbaceous ground cover $p = 0.061$, stem density $p = 0.244$). Similarly, soil texture did not represent as a significant contributor to the top model, regardless of which of the three soil texture percentages were included. Soil texture did not vary much across the sampled areas, with all samples being categorized as silt or silty loam (Fig. 2).

Four top models were averaged to form the final model for landscape-level variables (Table 1). All four variables were present in the final model, with available soil water storage and average annual precipitation being significant ($p < 0.05$; Table 2). Available soil water storage was positively correlated with *C. fodiens* presence, whereas average annual precipitation was negatively correlated with *C. fodiens* presence (Table 2). Models with landscape-level variables consistently ranked above the null model.

Discussion

Crayfish response to management

We developed both fine-scale and landscape-level models to assess the habitat preferences of burrowing crayfish. It was not expected that our sampling would yield only one species, *C. fodiens*, but this result allowed us to examine the habitat preferences of this species more closely. Across the sampled landscape, open-canopy habitat was the only significant fine-scale characteristic for burrow density. Open-canopy environments have been recorded as important habitats for several species (Welch 2006, Rhoden et al. 2016,

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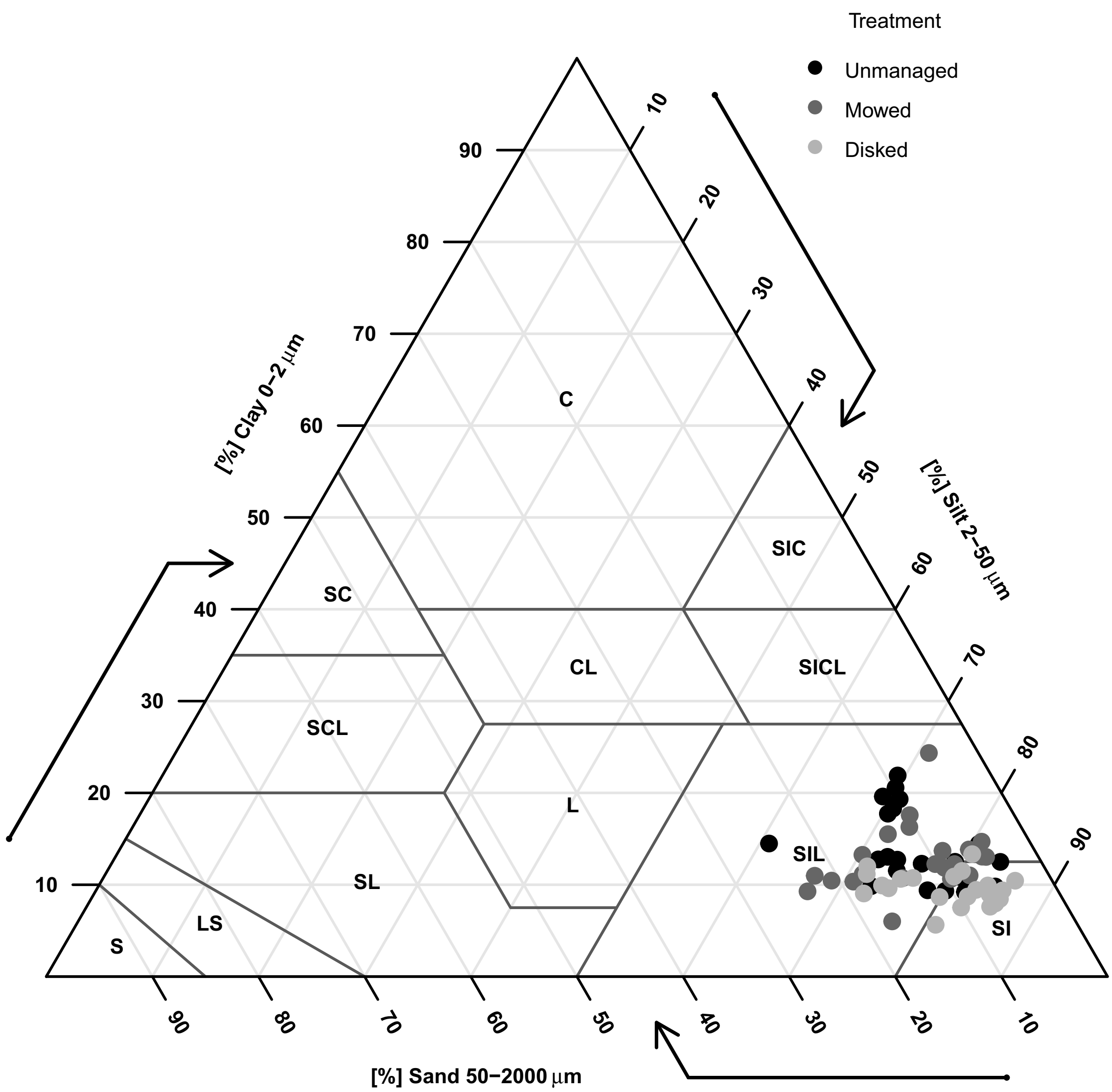

Fig. 2. Soil texture plot for soil samples collected at Duck Creek and Otter Slough Conservation Areas, Missouri, in spring 2021. Each symbol represents a transect and its shade denotes the vegetation treatment. Texture classes follow the United States Department of Agriculture classification system (Soil Survey Division Staff 1993). All soil samples collected were classified as silt (SI) or silty loam (SIL).

Table 2. Model averaged parameter estimates of the top models for *Creaserinus fodiens* presence in two conservation areas in Missouri. Bold values indicate significant results at $\alpha = 0.05$

Variable	Model averaged estimate (SE)	95% confidence limits	P > |z|
Available water storage	1.389 (0.598)	0.217, 2.561	**0.020**
Euclidean distance to stream	0.499 (0.327)	−0.142, 1.140	0.127
Average annual precipitation	−1.200 (0.540)	−2.258, −0.143	**0.026**
Elevation	0.265 (0.464)	−0.643, 1.174	0.567
Intercept	−0.105 (0.386)	−0.860, 0.651	0.786

Adams et al. 2021). *C. fodiens* did not exhibit a significant response to vegetation management; however, our data do show it had lower burrow densities in unmanaged areas. This is likely attributable to higher levels of canopy cover in unmanaged areas, often being the result of no vegetation management to impede succession. In unmanaged areas where canopy cover was lower, both active burrows and captured specimens were recorded. Adams et al. (2021) demonstrated a significant effect of vegetation but not vegetation management (mowing, mulching and prescribed burning) on *Creaserinus oryktes* in Mississippi. We split mechanical vegetation management into individual management practices to examine any fine-scale differences. It seems possible that primary burrowing crayfish are tolerant of the disturbance resulting from vegetation management and are responding largely to the resulting vegetation composition alone or in conjunction with other faunal responses to vegetation composition.

There was a significant effect of available soil water storage and precipitation on the presence or absence of *C. fodiens* burrows. Available water storage was positively correlated with burrow presence. Open canopy and high available water storage both indicate areas of wet seepage and higher soil moisture (Anderson et al. 1969, Gray et al. 2002). Precipitation was negatively correlated with burrow presence, although the average annual precipitation fluctuated

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by only 5 cm across the sampled areas. This may be an indicator that some primary burrowing crayfish prefer moist-soil areas but respond negatively to heavily saturated or flooded conditions.

Cross-taxa management on wetlands

The United States Fish and Wildlife Service National Wetlands Inventory estimates that there are *c.* 44.5 million ha of wetlands across the conterminous USA, with 94.7% of these being freshwater wetlands (Dahl 2011). Managing the 9.7 million ha of wetlands in the Mississippi Alluvial Valley requires regular mowing and/or disking to support perennial plant seed production (Covington et al. 2003). This practice promotes food and habitat for several seed-eating ducks and foraging birds such as herons, egrets and bitterns in moist-soil wetlands. Similarly, emergent marshes require mowing and/or disking to impede succession and to support emergent cover for wading birds such as rails, grebes and coots (Covington et al. 2003). Our results demonstrate that these open-canopy, moist-soil areas are key habitats for maintaining *C. fodiens* populations. Whereas macroinvertebrates are not actively managed on wetlands properties, aligning their management with waterfowl management could benefit both faunal groups.

The formation of subsurface burrows by crayfish leads to mixing of soil layers, leached nutrients being returned to the surface soil, increased aeration and improved subsurface water flow promoting plant growth (Bloomer et al. 2021). Moist-soil wetland managers typically do not plant seeds because seeds are already present in frequently flooded soils (Covington et al. 2003), so improved plant growth would help to maintain this resource. Similarly, native grass stand culm density is reduced when plant litter builds up. Burrowing crayfish are detritivores (Thoma & Armitage 2008, Grey & Jackson 2012) and can reduce autochthonous plant matter. Managed vegetation stands support a wide diversity of invertebrates that serve as a critical food source for migrating birds (Covington et al. 2003). Crayfish burrows support many invertebrate species including arthropods, nematodes, annelids and insects (Bloomer et al. 2021), providing habitats for these key food sources. The North American Waterfowl Management Plan highlights the importance of enhancing waterfowl habitats for productivity and resilience (North American Waterfowl Management Plan Committee 2012). Burrowing crayfish provide many benefits and should be considered to be a valuable resource on wetland properties.

The wide geographical range of *C. fodiens* combined with its open-canopy association and ability to inhabit disturbed soils classify it as a habitat generalist (Loughman et al. 2012). Other generalist burrowing species have been found in open and forested habitats across their ranges (Hobbs & Rewolinski 1985, Hobbs & Whiteman 1991, McGrath 1994). These species seem to present fewer fine-scale habitat associations, which likely facilitates their ability to occupy a large geographical range. Habitat specialists are suggested to be less tolerant of human disturbance (Loughman et al. 2012). However, habitat specialists have also been demonstrated to thrive in mechanically managed areas (Adams et al. 2021) and mowed roadside ditches (Rhoden et al. 2016). From this literature, we expect that the management practices that reduced canopy cover and benefitted *C. fodiens* here would also benefit other burrowing species, both generalist and specialist.

However, there are other wetlands management practices that have not been evaluated. Hydrologic manipulation is a major wetlands management practice using structures such as dikes, diversions and sloughs to control flooding depth, duration and timing (Covington et al. 2003). Water-level manipulations attract foraging birds through guaranteed water supply, increased moist-soil vegetation, the reducing of predation and the trapping of edible invertebrates (Fredrickson 1991). During our study, 4 workers searched for 45 min in an area of managed waterfowl habitat that is manually flooded for *c.* 7 months of the year. We observed no sign of crayfish burrows, despite such burrows being present in nearby non-flooded areas. The impact of the timing and duration of hydrologic manipulation must be evaluated before we can assert that all waterfowl management is beneficial to burrowing crayfish.

Taylor et al. (2019) emphasized that incorporating crayfish into conservation planning and habitat management in protected areas is a key strategy to improve US conservation efforts for crayfish. Maintaining open-canopy, moist-soil areas in wetlands is key to conserving primary burrowing crayfish and to halting population declines. Integrating crayfish management with some aspects of waterfowl management may facilitate this. *C. fodiens* is the most widespread primary burrowing species in the USA, so the conservation efforts proposed here apply beyond the locality of this study. Our data demonstrate that some wetland management practices directed towards unrelated taxonomic groups may be beneficial to non-target organisms. Future efforts must examine other burrowing crayfish species and land management practices in wetlands in order to evaluate whether management integration can be a widespread conservation solution.

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Conflict of interest. The authors declare none.

Ethical standards. None.

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