

Highway to heaven? Roadsides as preferred habitat for two narrowly endemic crayfish

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Abstract: Roadside ditches can have attributes that are beneficial or detrimental for animal persistence. Investigators have found mostly negative effects on fauna that inhabit roadside ditches. However, we think the microhabitat found in the roadside ditches could be beneficial to 2 narrowly endemic habitat specialists. We tested this prediction by collecting habitat data for 2 primary burrowing crayfish species, *Fallicambarus harpi* and *Procambarus reimeri*, in the Ouachita Mountains Ecoregion of Arkansas. We analyzed the data with generalized linear mixed models. Our analysis revealed that canopy cover and the presence of hydrophilic sedges are important factors in predicting crayfish abundance across the landscape. We conclude that the microhabitat of roadside ditches can be beneficial to the persistence of these 2 narrowly endemic habitat specialists.

Key words: Arkansas, burrowing crayfish, *Fallicambarus harpi*, Ouachita Mountains, *Procambarus reimeri*, road

Human-made linear right-of-ways (ROWs), such as roads, roadside ditches, public utility easements, and railroad lines, and their maintenance usually have a negative effect on habitat and life-history attributes of animal populations (Rytwinski and Fahrig 2013). ROWs are dramatically altered landscape features that can disrupt wildlife movements (Richardson et al. 1997), fragment habitat (Andrews 1990), and directly cause mortality (Ashley and Robinson 1996, Lode 2000). Roads can act as a physical barrier and can be a behavioral barrier to movement (Oxley et al. 1974, Riley et al. 2006). In addition, the particulate matter emissions from vehicles can be a negative attribute of roadside microhabitat environments (Thorpe and Harrison 2008). Conversely, roadsides can have positive attributes to plant and animal persistence. They can act as corridors for native and nonnative species dispersion (Gelbard and Belnap 2003) and can support higher animal densities and diversity than in surrounding habitat (Adams and Geis 1983). The interactions observed in these areas are a result of the construction and maintenance of the linear ROW.

The objectives of roadside maintenance activities have changed very little since the conversion from trail to road and include: maintaining hydraulic capacity of ditches, eliminating vegetative obstructions, and providing wildlife habitat where compatible with roadway traffic (Berger 2005). This environment is disturbed constantly by roadside maintenance (e.g., mowing, spraying herbicide, tree cutting) and remains open, resulting in habitats that resemble early suc-

cessional stages in natural landscapes. Thus, roadside maintenance can lead to open habitat within a matrix of forested habitat (Watkins et al. 2003), an alteration that can be both beneficial and detrimental to the persistence of wildlife.

The characteristics of animal populations that are vulnerable to negative road effects have been documented as: having high intrinsic mobility, high migration potential, multiple resource needs, low density/large area requirements, and a low reproductive rate; being a forest interior species; and displaying a behavioral avoidance of roads (Forman et al. 2003). Animals that display these traits are inhibited by the physical presence of the road and by road effects associated with the ROW, such as edge effects. Investigators have studied the responses of various biotic communities to ROWs (see Spellerberg 1998), but the interaction of biotic communities and ROWs is still not fully understood. Fahrig and Rytwinski (2009) reviewed biotic communities and roadsides and found that 59% of interactions resulted in a negative effect on animal abundance. The minority of animal populations that experience some positive effects from roadsides have a small territory range, have a high reproductive rate, and are small bodied. Investigators have shown a positive response from fauna that exhibit these life-history characteristics (Peris and Pescador 2004, Rosa and Bissonette 2007, Ward et al. 2008). Small populations of endemic habitat specialists often experience negative effects from ROW construction and maintenance (e.g., Altrichter

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and Boaglio 2004, Pocock and Lawrence 2005, Semlitsch et al. 2007). However, construction and maintenance of ROWs could benefit directly some narrowly endemic habitat-specialist taxa by creating suitable habitat (Forman et al. 2003). One such taxon experiencing these benefits could be North American burrowing crayfishes.

All crayfishes are hypothesized to have the ability to construct refugia by way of burrowing into the soil or substrate (Hobbs 1981, Berrill and Chenoweth 1982). Construction of burrows and open space within them, allows access to ground or atmospheric water for O₂ extraction. Hobbs (1981) described 3 classes of burrowing crayfishes based on differences in natural history: tertiary, secondary, and primary burrowers. Tertiary burrowers dig shallow burrows only to escape frost or seek shelter and when the body of water they inhabit dries up. Secondary burrowers spend much of their lives in their burrows; however, they do move out into open water occasionally, and their burrows normally have a connection to an open, permanent water body. Primary burrowing crayfishes spend their complete life cycle underground. Primary burrowers leave their burrows only to forage and find a mate (Hobbs 1981), so their burrows are rarely tied to permanent open water. Rather, these species use subsurface ground water for moisture and oxygenation.

Prior to the 20th century, the habitat in which some primary burrowing crayfishes occurred naturally could have been functionally similar to some human-made ROWs. Specifically, human-made ROWs, such as roadsides, could imitate the hypothesized natural habitat of these animals by creating a landscape that is void of trees, supports a perched water table, and maintains an open, low-grass microhabitat. To test that hypothesis, we examined 2 narrowly endemic habitat specialists, *Fallicambarus harpi* and *Procambarus reimeri*, known from the Ouachita Mountains Ecoregion (OME) of western Arkansas (Woods et al. 2004). These species are vulnerable to population declines and are currently listed as endangered (*P. reimeri*) and vulnerable (*F. harpi*) by Taylor et al. (2007). Categories and criteria of Taylor et al. (2007) follow those established by the American Fisheries Society Endangered Species Committee (Williams et al. 1993, Warren et al. 2000). In addition, these species were included in a recent petition filed by the privately funded Center for Biological Diversity for protection under the US Endangered Species Act. Both species are known historically from <40 individual sampling sites in restricted areas of the OME. Robison and Crump (2004) reported *F. harpi* as occurring in wet grassy areas that often had abundant sedges and grasslands such as ditches and pastures. Robison (2008) reported the habitat in which *P. reimeri* was observed as wet seepage areas and roadside ditches. Based on historic accounts of both species, we predicted some habitat attributes would be more important than others, particularly the presence of sedges and open canopy. We also expected soil composition would be a strong driver of burrow placement. Soil cues are im-

portant for other burrowing crayfishes (e.g., Grow and Merchant 1980, Barbaresi et al. 2004, Helms et al. 2013). To evaluate whether *F. harpi* and *P. reimeri* could be experiencing a positive effect from the microhabitat in ROWs, we developed a study based on extensive field sampling and habitat modeling of multiple variables to determine the fine-scale habitat preferences of both *F. harpi* and *P. reimeri* in relation to ROWs.

METHODS

Study site

Our study sites were situated in the Ouachita and Caddo River drainages of southwestern Arkansas. We focused on 5 counties in the OME that encompass the entire known range of *F. harpi* and *P. reimeri* (Fig. 1). The OME harbors the highest diversity of primary burrowing crayfishes in the state. Six species occur there: *F. harpi*, *Fallicambarus jeanae*, *Fallicambarus strawni*, *Procambarus liberorum*, *Procambarus parasimulans*, and *P. reimeri*.

The Ouachita Mountains are composed of parallel, folded east–west ridges underlain by shale and sandstone (Miser 1929). The soils of this region are generally categorized as silty clay and silty loam (Hlass et al. 1998). The most common forest community is mixed pine–hardwood; however, remnant pine–bluestem communities do exist (Phillips and Marion 2005). Logging and recreation make up the major land uses of this area, and pastureland and hay fields are found in the broader valleys (Woods et al. 2004). We focused our sampling effort in these broader valleys.

Field collections

All sampling took place in April 2014 because April is the peak activity period for both species (Robison and Crump 2004, Robison 2008) and, thus, would result in highest species detection. We visited known historical locations for both *F. harpi* and *P. reimeri*. The databases of the Illinois Natural History Survey Crustacean Collection, National Museum of Natural History Invertebrate Zoology Collection, and Arkansas Department of Natural Heritage were used to identify these locations. For each species, we selected historic localities that were accessible and could be validated with geographic positioning information. At each sampling site we positioned three to six 50-m transects ≤100 m from the initial transect. The initial transects were parallel to the road and within the ROW. We placed the initial transect at each sampling site where burrows were present, ensuring the initial transect was situated at the historical museum location. We laid out each subsequent transect and then checked for standing water along the transect. All transects were delineated with a fiberglass measuring tape. After we obtained a global positioning system location and azimuth at the 0-m mark, we placed a 1-m² polyvinyl chloride quadrat over the tape every 10 m, which resulted in six 1-m² quadrats/50-m transect. After

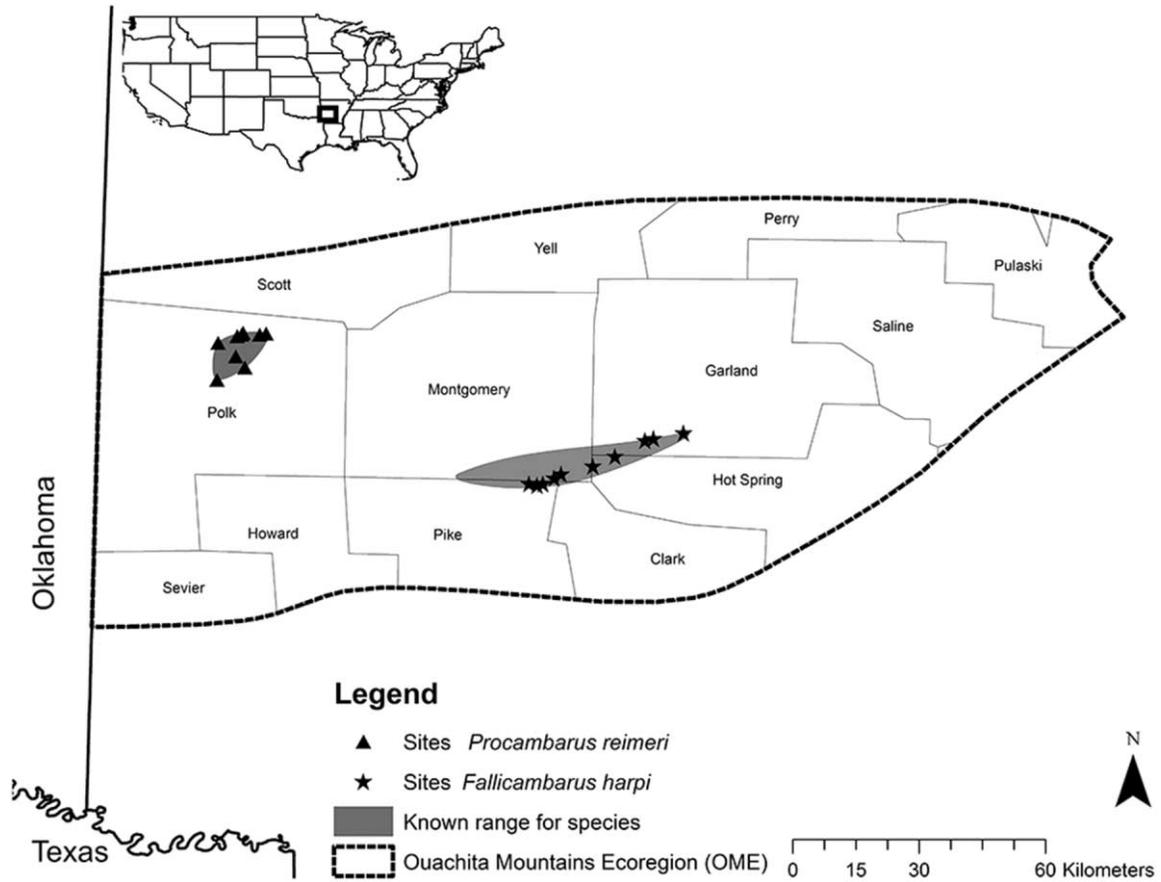


Figure 1. Sites sampled for *Fallicambarus harpi* and *Procambarus reimeri* in Arkansas.

we completed the initial transect, we completed the remaining 2 to 5 transects in adjacent habitat in the same manner. We decided the number of transects to be sampled at each site based on habitat heterogeneity. If a site was homogenous, we sampled fewer transects to increase the number of sampling sites that could be visited during our sampling window. We defined adjacent habitat as having significantly more or less canopy cover, seemingly different soil moisture content, higher or lower elevation, or a different dominant vegetation type compared with the initial transect. We excavated burrows at each sampling site and along each transect to ensure any burrows counted at a sampling site harbored the target species. We collected voucher specimens of each target species from all sites with burrows present and deposited them in the Illinois Natural History Survey Crustacean Collection.

Habitat variables

We collected the following habitat variables within each 1-m² quadrat: % tree canopy cover, % herbaceous ground cover, stem density, number of burrows, and the presence

or absence of hydrophilic sedges (Table S1). We estimated % tree canopy cover with a concave spherical densiometer (model C; Robert E. Lemmon, Forest Densiometers, Bartlesville, Oklahoma). We calculated % herbaceous ground cover by inverting the concave spherical densiometer over the 1-m² quadrat. We calculated stem density by counting the stems within a smaller (100-cm²) quadrat placed within the upper right-hand corner of each 1-m² quadrat. We scored the presence vs absence of hydrophilic sedges by recording the presence or absence of herbaceous plants that had 3-ranked leaves, an angular stem, and a spiked fruiting body. At each transect, we collected 3 evenly spaced soil samples with a soil probe (AMS 7/8-in. [2.2-cm] diameter open-end probe; AMS, American Falls, Idaho) at a minimum depth of 43 cm and a maximum depth of 66 cm. These depths reflect the column of soil the crayfishes are using for burrow construction (Robison and Crump 2004 and validated in the field). We analyzed the soil samples with laser diffraction on a Malvern Mastersizer 3000 (Malvern Instruments, Malvern, UK) to obtain a % composition (sand, silt, and clay) for each sample. We computed the isometric log-ratio transformation for these data (Egoz-

cue et al. 2003). We constructed a soil texture plot with the package *soiltexture* in R (version 3.1.1; R Project for Statistical Computing, Vienna, Austria) (Moeys 2015). The selected habitat variables reflect habitat characteristics associated with *F. harpi* (Robison and Crump 2004) and *P. reimeri* (Robison 2008), other primary burrowing crayfish species (Hobbs 1981, Welch and Eversole 2006, Loughman et al. 2012), and biological intuition. The habitat variables and a description of each model term used in the statistical analysis are shown in Table 1.

Upon returning from the field we mapped the quadrat locations in ArcGIS (version 10.2; Environmental Systems Research Institute, Redlands, California). We then calculated the following habitat variables for each quadrat with ArcGIS: elevation, distance to nearest water body, compound topographic index value (CTI), and solar radiation value. We measured elevation as the height in meters above sea level and distance to nearest water body as the Euclidean distance from all permanent water bodies. We assessed CTI with the Geomorphometry and Gradient Metrics toolbox for ArcGIS (version a1.0; Evans et al. 2010). This metric is a function of both the slope and the upstream contributing area per unit width orthogonal to the flow direction. We measured solar radiation by calculating the watt-hour (Wh)/m² of the delineated sampling area. We calculated all ArcGIS values with digital elevation maps (National Elevation Dataset, 1/3 arc-second; <http://ned.usgs.gov/>) and surface-water maps (National Hydrography Dataset; <http://nhd.usgs.gov/index.html>) at a resolution of 10 m in an attempt to minimize autocorrelation. We combined the habitat variables collected in the field and those calculated with ArcGIS into 1 data set for a fine-scale analysis of habitat features affecting crayfish burrow placement on the landscape.

Modeling analysis

We conducted all fine-scale statistical analyses in R. We made the isometric log-ratio transformations with the package *compositions* (van den Boogaart et al. 2014). We used generalized linear mixed models to analyze the data (package *lme4*; Bates et al. 2014). The response variable in each model was the number of burrows within each 1-m² quadrat and was modeled with a Poisson error distribution and log link. We modeled burrow counts separately for each species. To account for potential site effects, we modeled transects nested within sites as a random effect in each model. We scaled and centered all habitat variables by subtracting the variable mean from each respective value and dividing by the standard deviation (SD) of that variable. We assessed model convergence and fit and then adjusted the optimization algorithm as needed. We did not include covariates that had a Spearman correlation coefficient of >0.60 in the confined candidate model set. The full candidate model set and each hypothesis tested is shown in Table 2. We compared candidate models with Akaike Information Criterion corrected for small sample sizes (AICc; Akaike 1974). We examined the relative support for each model and calculated unbiased model-averaged parameter estimates from the top models ($\Delta\text{AICc} < 4$) with the package *MuMIn* (Barton 2014) by means of model selection and averaging methods described by Burnham and Anderson (2002) and Lukacs et al. (2009).

RESULTS

Field collections

Our search of museum databases resulted in 57 unique historic capture records (24 for *F. harpi* and 33 for *P. reimeri*). The records ranged from 1967 to 2008, and the

Table 1. Variables and their descriptions for a generalized linear mixed-model analysis of the habitat of 2 primary burrowing crayfishes in Arkansas (*Fallicambarus harpi* and *Procambarus reimeri*). Quadrats were 1 m².

Variable	Description
Water_trans	Presence of standing water in the length of the 50-m transect (binary: yes/no)
Sedge	Presence of hydrophilic sedge in quadrat (binary: yes/no)
Canopy	% tree canopy cover taken at each quadrat
Herb	% herbaceous ground cover taken at each quadrat
Stem	Stem-density count taken at each quadrat
Elevation	Elevation calculated at each quadrat location (National Elevation Dataset, resolution 10 m; http://ned.usgs.gov/)
Solar	Incoming solar radiation value (watt-hour/m ²) calculated at each quadrat location based on direct and diffuse insolation from the unobstructed sky directions (ArcGIS; Environmental Systems Research Institute, Redlands, California)
Water_dist	Euclidean distance to nearest water body calculated for each quadrat location (National Hydrography Dataset; http://nhd.usgs.gov/index.html)
CTI	Compound topographic index value calculated for each quadrat location (Evans et al. 2010)
Soil1, Soil2	Transformed soil composition (% sand, silt, clay) value calculated for each soil sample (van den Boogaart et al. 2014)

Table 2. Candidate models and hypotheses tested in the generalized linear mixed-model analysis for *Fallicambarus harpi* and *Procambarus reimeri* in Arkansas. The response variable used in each model was burrow abundance in each 1-m² quadrat. See Table 1 for variable names.

Model name:	Variables	Hypothesis
Mod 1(global)	Water_trans + sedge + canopy + herb + stem + elevation + solar + water_dist + CTI + soil1 + soil2	Crayfish selection based on transect- and quadrat-level wetness characteristics, canopy cover, herbaceous community, erosion potential, topographic position, solar radiation potential, and soil cues
Mod 2	Canopy + sedge	Crayfish selection based on canopy cover and quadrat-level wetness
Mod 3	Water_trans + sedge + solar + water_dist	Crayfish selection based on transect- and quadrat-level wetness characteristics, solar radiation potential, and topographic position
Mod 4	Water_trans + sedge + CTI	Crayfish selection based on transect- and quadrat-level wetness characteristics and topographic position
Mod 5	Water_dist + CTI	Crayfish selection based on topographic position
Mod 6	Solar + CTI	Crayfish selection based on solar radiation potential and topographic position
Mod 7	Elevation + water_dist	Crayfish selection based on topographic position
Mod 8	Sedge + stem	Crayfish selection based on herbaceous community
Mod 9	Canopy + herb	Crayfish selection based on canopy and herbaceous community
Mod 10	Herb + soil1 + soil2	Crayfish selection based on herbaceous community and soil cues
Mod 11	Canopy + soil1 + soil2 + sedge	Crayfish selection based on canopy cover, soil cues, and quadrat-level wetness
Mod 12	Canopy + solar + soil1 + soil2	Crayfish selection based on canopy cover, solar radiation potential, and soil cues
Mod 13	Canopy + sedge + stem	Crayfish selection based on canopy cover, quadrat-level wetness, and erosion potential
Mod 14	Soil1 + soil2 + water_trans	Crayfish selection based on soil cues and transect-level wetness
Mod 15	Canopy	Crayfish selection based on canopy cover
Mod 16	Soil1 + soil2	Crayfish selection based on soil cues
Mod 17	Solar	Crayfish selection based on solar radiation potential

oldest record we visited was from 1973. We sampled 11 of these localities (35 transects, 210 quadrats) for *F. harpi* and 9 sites (37 transects, 222 quadrats) for *P. reimeri*. Most (75%) of these localities were in the ROW of secondary, local, and private roads. Other sampling sites (25%) were situated in yards, pastures, and adjacent habitat farther from the ROW (up to 90 m). *Fallicambarus harpi* was present at all 11 sites (20 transects, 58 quadrats). *Procambarus reimeri* was present at 8 of the 9 sites sampled (23 transects, 52 quadrats). In total, we counted 143 burrows for *F. harpi* and 71 burrows for *P. reimeri*.

Modeling analysis

Fallicambarus harpi and *P. reimeri* had similar patterns of habitat selection. For both species, canopy cover was the most important habitat variable, and it was present in all

top models ($\Delta AICc < 4$; Table 3). Model-averaged parameter estimates for both species are shown in Table 4. Canopy cover was negatively associated with the number of burrows in a quadrat (Figs 2A, 3A). The presence of hydrophilic sedges was positively associated with the number of burrows in a quadrat (Figs 2B, 3B). The transformed soil variables and stem density variable were also present in the top models. Burrows were generally present in quadrats with little to no canopy cover (mean \pm SD, 4.4% \pm 17.7, $n = 110$). No burrow was observed in a quadrat with complete canopy cover (100%). Sedges were present in 83% of the quadrats that harbored burrows of either species ($n = 110$).

DISCUSSION

We developed a suite of models to assess our predictions regarding the habitat preferences of *F. harpi* and

Table 3. Model name, number of model parameters (K), Akaike's Information Criterion adjusted for small sample size (AICc), difference in AICc (ΔAICc), Akaike weights (w_i), and log likelihood (LL) for the top habitat models ($\Delta\text{AICc} < 4$) from a suite of variables modeled with a generalized linear mixed-model analysis for 2 primary burrowing crayfish species, *Fallicambarus harpi* ($n = 210$ quadrats) and *Procambarus reimeri* ($n = 222$ quadrats) in Arkansas. See Tables 1 and 2 for a description of each model and the variables included.

Model	K	AICc	ΔAICc	w_i	LL
<i>Fallicambarus harpi</i>					
Mod 11	7	374.63	0	0.50	-180.04
Mod 2	5	375.99	1.36	0.26	-182.85
Mod 13	6	377.92	3.29	0.10	-182.76
<i>Procambarus reimeri</i>					
Mod 2	5	285.6	0	0.67	-137.66
Mod 13	6	287.7	2.11	0.23	-137.66
Mod 11	7	289.42	3.82	0.1	-137.45

P. reimeri. We found support for some of our predictions, whereas some results were counterintuitive. Open-canopy habitat and the presence of sedges were important for burrow placement across the sampled landscape. Our predictions that these variables would be preferred by both species of crayfish were supported by the models fitted with generalized linear mixed-model analysis. The presence of hydrophilic sedges is an indication of a seepage area or that the water table is relatively close to the ground surface (Schütz 2000). The absence of tree canopy cover also

contributes to these wet seepage areas (Eastham et al. 1994). Our hypothesis that soil would be a strong predictor was not supported. This outcome probably was a result of our sampling procedure. We collected soil samples that fell into only 3 distinct soil textural classes (silt loam, loam, and sandy loam; Fig. 4), which did not capture the variation seen across the entire OME. We think, however, that our findings point to the preference of ROW-like habitat for *F. harpi* and *P. reimeri*. The habitat in which animals were most abundant was treeless, wet seepage areas with abundant low grasses and sedges. The soil composition at these occupied sites was primarily loam and silt loam (Soil Survey Division Staff 1993; 90% of *F. harpi* quadrats, 92% of *P. reimeri* quadrats). The burrows of *F. harpi* and *P. reimeri* were complex, 0.5–1 m in depth, and connected to groundwater. Our results highlight the specific importance of these wet, open-canopy habitats as a preferred environment for both species.

Previous studies of other primary burrowing crayfish species have revealed the existence of habitat specialists and habitat generalists. Specialist species occur in habitats ranging from pitcher plant bogs (*Fallicambarus gordonii* [Johnston and Figiel 1997]) to sand ridges (*Distocambarus crockeri* [Welch and Eversole 2006]), whereas generalist species can be found in both forested floodplains and open habitat throughout their respective ranges: *Procambarus gracilis* (Hobbs and Rewolinski 1985), *Fallicambarus devastator* (Hobbs and Whiteman 1991), *Fallicambarus fodiens* (Norrocky 1991), *Cambarus catagius* (McGrath 1994), *Cambarus dubius* (Loughman 2010), and *Cambarus thomai* (Loughman et al. 2012). Based on the modeling and field

Table 4. Unbiased model-averaged parameter estimates of the top models (Table 3) for 2 primary burrowing crayfish species (*Fallicambarus harpi* and *Procambarus reimeri*) in Arkansas. See Table 1 for a description of the variables included. Sedge1 = presence of sedge in quadrat, CL = confidence limits.

Species and variable	Model-averaged estimate (SE)	95% CL	$p > z $
<i>Fallicambarus harpi</i>			
Canopy	-1.003 (0.3863)	-1.761, -0.246	0.009
Sedge1	0.546 (0.239)	0.077, 1.015	0.071
Stem	0.045 (0.105)	-0.161, 0.250	0.899
Soil1	0.144 (0.125)	-0.102, 0.388	0.509
Soil2	-0.293 (0.127)	-0.542, -0.044	0.364
Intercept	-2.183 (0.485)	-3.135, -1.232	—
<i>Procambarus reimeri</i>			
Canopy	-1.317 (0.468)	-2.234, -0.401	0.005
Sedge1	1.727 (0.474)	0.797, 2.656	0.0002
Stem	0.003 (0.073)	-0.281, 0.306	0.968
Soil1	0.003 (0.047)	-0.258, 0.320	0.948
Soil2	0.007 (0.059)	-0.272, 0.414	0.905
Intercept	-3.135 (0.513)	-4.140, -2.130	—

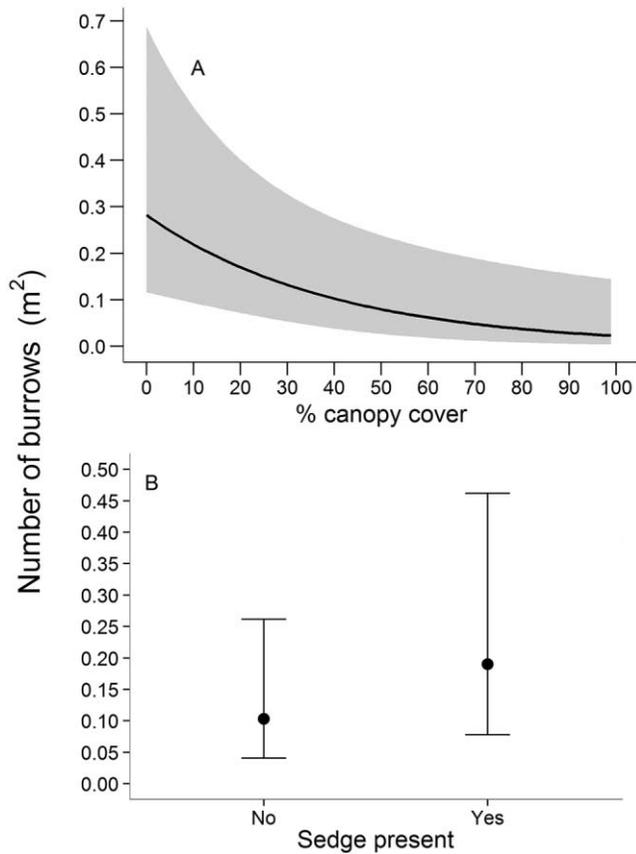


Figure 2. A.—Estimated number of *Fallicambarus harpi* burrows/m² in relation to the % tree canopy cover over a quadrat. The shaded area indicates the 95% confidence interval (CI) of burrow counts in relation to the variable canopy. B.—Mean (95% CI) number of burrows in quadrats with and without sedges.

observations, *F. harpi* and *P. reimeri* can be considered habitat specialists. They occur in wet, open herbaceous areas and not in the adjacent forested habitat. We think the microhabitat of the roadside ditch is acting as suitable habitat for these specialists within a matrix of unsuitable habitat.

We sampled transects adjacent to known localities to better model habitat use and selection for each species. The habitats sampled by these transects generally differed in composition from the ROW (Table S1) but were spatially proximate so as to be accessible to crayfish. These sites composed 25% of the sampling locations and were not in the ROW. We designed this sampling scheme with the knowledge that it would be unnecessary and cost ineffective to sample the entirety of the OME randomly. Primary burrowing crayfish rarely, if ever, inhabit permanent open water (Hobbs 1981), such as streams, lakes, and swamps, or high-gradient slopes found in the larger OME. A review of over 2000 freshwater crayfish collections made

in the state of Arkansas (Illinois Natural History Survey Crustacean Collection and National Museum of Natural History Invertebrate Zoology Collection) revealed no observations of *F. harpi* or *P. reimeri* in either of these habitat types. Thus, we think the microhabitat available to primary burrowing crayfish is spatially restricted because of their life-history characteristics (Hobbs 1981), and those available habitats were represented in our sampling design.

The microhabitat found in roadside ditches where these animals occur is a result of the physical presence of the road and roadside maintenance. The surface of the road is less permeable than the surrounding habitat, which diverts precipitation into the surrounding terrain (MacDonald et al. 2001). The roadside ditch also intercepts groundwater flow, adding more water to the roadside microhabitat (Forman et al. 2003). Roadside maintenance halts succession by removing woody stems and constantly disturbs the herbaceous community with mowing and herbicide application. The removal of woody stems also increases the soil mois-

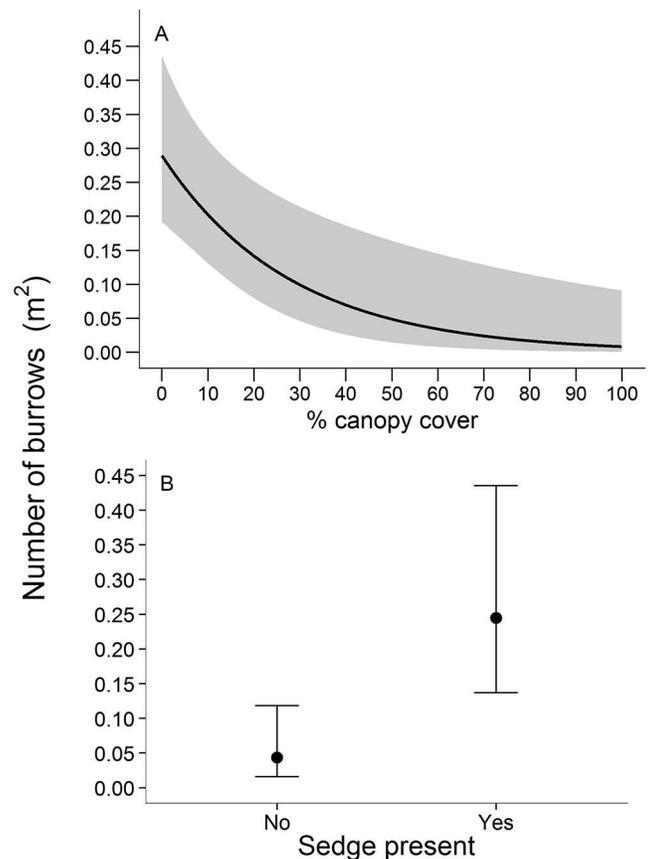


Figure 3. A.—Estimated number of *Procambarus reimeri* burrows/m² in relation to the % tree canopy cover over a quadrat. The shaded area indicates the 95% confidence interval (CI) of burrow counts in relation to the variable canopy. B.—Mean (95% CI) number of burrows in quadrats with and without sedges.

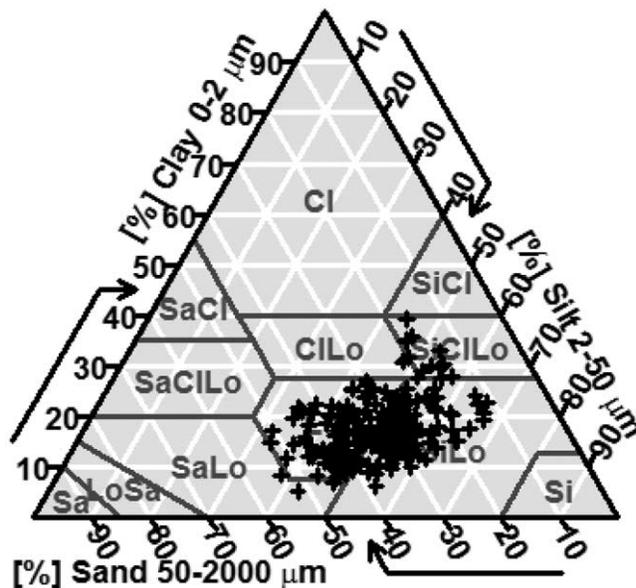


Figure 4. Soil texture plot for soil samples collected in the spring 2014. CI = clay, SiCl = silty clay, SaCl = sandy clay, CILo = clay loam, SiCILo = silty clay loam, SaCILo = sandy clay loam, Lo = loam, SiLo = silty loam, SaLo = sandy loam, Si = silt, Sa = sand, and LoSa = loamy sand. Texture classes follow those of US Department of Agriculture (Soil Survey Division Staff 1993). Classes obscured by data points are loam (lower center of figure) and silty loam (lower right of figure).

ture in the roadside habitat (Eastham et al. 1994) because woody stems have deeper root systems and are capable of transpiring more water from the soil than are grasses. Through these road-maintenance activities, the ROW habitat is uniformly distributed where the road occurs. These attributes of the roadside appear to have created suitable habitat for these 2 species of primary burrowing crayfishes.

The characteristics of animal populations that are vulnerable to negative road effects have been documented as: high level of mobility, behavioral avoidance of roads, and habitat generalist or forest interior species. The negative responses observed in the biota that have these characteristics are not seen in *F. harpi* or *P. reimeri*. These 2 species do not show a high level of mobility or a behavioral avoidance of roads: some of the sites revisited in our study were first discovered >40 y ago. These animals are not perceived as being habitat generalists or forest interior species. They were observed in open, wet, grassy areas, which suggests these species are habitat specialists within the broader matrix of forested habitat that dominates the OME. They may also be avoiding other direct negative effects of inhabiting ROWs by spending most of their life underground. Other species of burrowing crayfishes have been observed evading the effects of pesticide use by occupying a buffer zone within their burrows during pesticide application (Sommer 1983).

Our findings add to the understanding of the interactions between ROWs and the biota that live within them. Previous research has shown positive and negative responses of biota to ROWs (e.g., Adams and Geis 1983, Forman et al. 2003, Fahrig and Rytwinski 2009). Our study is the first to show a positive interaction between a narrowly endemic habitat specialist and a ROW habitat that is commonly seen as highly altered and detrimental to endemic wildlife populations. We are confident that we captured different potential habitat types available to *F. harpi* and *P. reimeri* by sampling the adjacent habitat. The adjacent habitats were out of the ROW and generally did not have the habitat characteristics of the roadside ditch. We think these crayfish prefer the ROW microhabitat because of the lack of canopy and presence of sedges, which presents a moist, low-herbaceous environment. These data support the benefit of ROWs to the persistence of these narrowly endemic habitat specialists. The use of this habitat by these species could also encourage dispersal along these linear corridors. Future work is needed to assess this possibility and to investigate locations within the OME within and well beyond the roadside ditch, where these animals are not known to occur.

ACKNOWLEDGEMENTS

We thank Brian Wagner, Josh Seagraves, Andrea Daniel, Allison Fowler, Benjamin Thesing, and Justin Stroman for permitting and field assistance. Special thanks to Sarah Tomke and Dan Wylie for field assistance. This work was funded with a State Wildlife Grant from the Arkansas Game and Fish Commission. Thanks to Mike Dreslik and Robert Schooley for help with the initial study design.

LITERATURE CITED

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